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A NEW FLYING LIZARD FROM THE SANGIHE ARCHIPELAGO, INDONESIA

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ABSTRACT. A new species of *Draco,* characterized by small size (to 75 mm SVL), reduced sexual dimorphism, somber coloration, five ribs in patagium, and eight to ten postrostrals, is described from Pulau Biaro, southernmost isle of Kepulauan Sangihe, *ca* 60 km north of the northeast tip of Minahasa, Sulawesi Utara.

Spanning some 450 km between Sulawesi and Mindanao, forming the northwestern limit of the Molucca Sea, are more than 40 islands on 15 submarine banks. Those closest to Sulawesi are named for their largest member: Kepulauan Sangihe—the Sangihe Archipelago. The southernmost of these, some 60 km northeast of Ponto do Celebres, and about 25 km from the next nearest land (Ruang), is the isle of Biaro. Like its sisters, Biaro is of volcanic origin. I suspect it arose just where we find it today, did not drift there from somewhere else, and has never had any terrestrial connection to any other land area.

The flying lizards, genus *Draco,* recently have been reviewed by Musters (1983) and Inger (1983). Their views are disparate. Only Musters admits *Draco* in the Sangihe Archipelago. He says *D. volans boschmai* is "perhaps on the Kepulauan Sangihe." He examined no specimens from these islands and only one *volans* from Sulawesi (that from Macassar in the extreme southwest).

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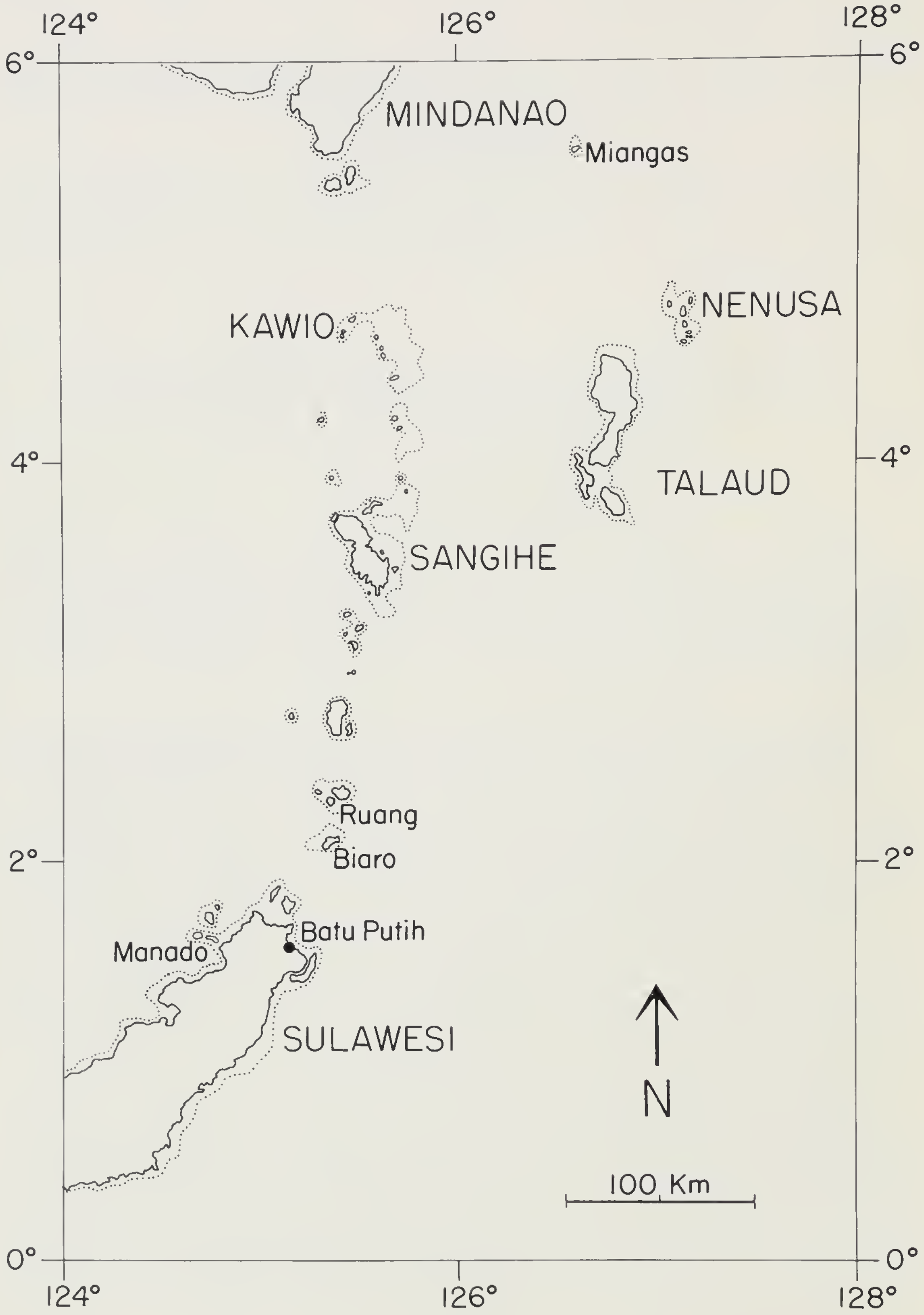
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Figure 1. The northwestern Molucca Sea showing the islands and banks (200 meter depth) and the locations of places mentioned in the text.

After carefully studying both papers and examining many specimens at the Museum of Comparative Zoology, I conclude that our knowledge of *Draco* today is similar to our knowledge of *Anolis* in 1950. Nevertheless, I have returned from Biaro with 22 specimens of a *Draco* so distinctive that I have no hesitation in describing it as new.

Draco biaro sp. nov.
(Fig. 2)

Type. MCZ 170898.

Type Locality. Pulau Biaro, Kepulauan Sangihe, Indonesia. Bernard F. Page coll., 4 April 1986. See Figure 1.

Paratypes. MCZ 170899–170919, same locality as the type; B. Page, J. Lazell, and local children coll., 4 April 1986.

Diagnosis. A small species of *Draco,* adults to 75 mm SVL; five ribs in patagium; nostrils pointing laterally; most (90%) with small scales covering tympanum; four or five incisors (Inger's method); six to eight supralabials (73% have seven); eight to ten scales bordering rostral (64% have nine); male throat fan small, 55 to 82% of head length (Musters' method) in adult males; coloration in life of both sexes somber, patagium sooty to slaty grey above with 15 to 20 sublongitudinal to subradiate narrow light grey streaks.

Description of the Type. Adult male, 73 mm SVL, with a complete tail 145 mm (199% SVL). There are eight weakly keeled supralabials and nine scales border the rostral. The tympanum is clothed in small scales. The throat fan is 71% of head length, hooked distally, and blunt at the tip. See Figure 2.

The dorsals are smooth to weakly keeled; there are 15 in the standard distance (tip of snout to center of eye) at midbody. The ventrals are sharply keeled; there are 16 in the standard distance at midbody. There are 27 subdigital lamellae beneath the fourth toe of the pes, counting from that toe's separation from the third toe.

There are no thornlike supraciliaries although a few anterior supraciliaries are enlarged and keeled. The Y-shaped arrangement of keeled snout scales is interrupted and only vaguely discernible. The lappets are edged by somewhat enlarged scales, but the throat

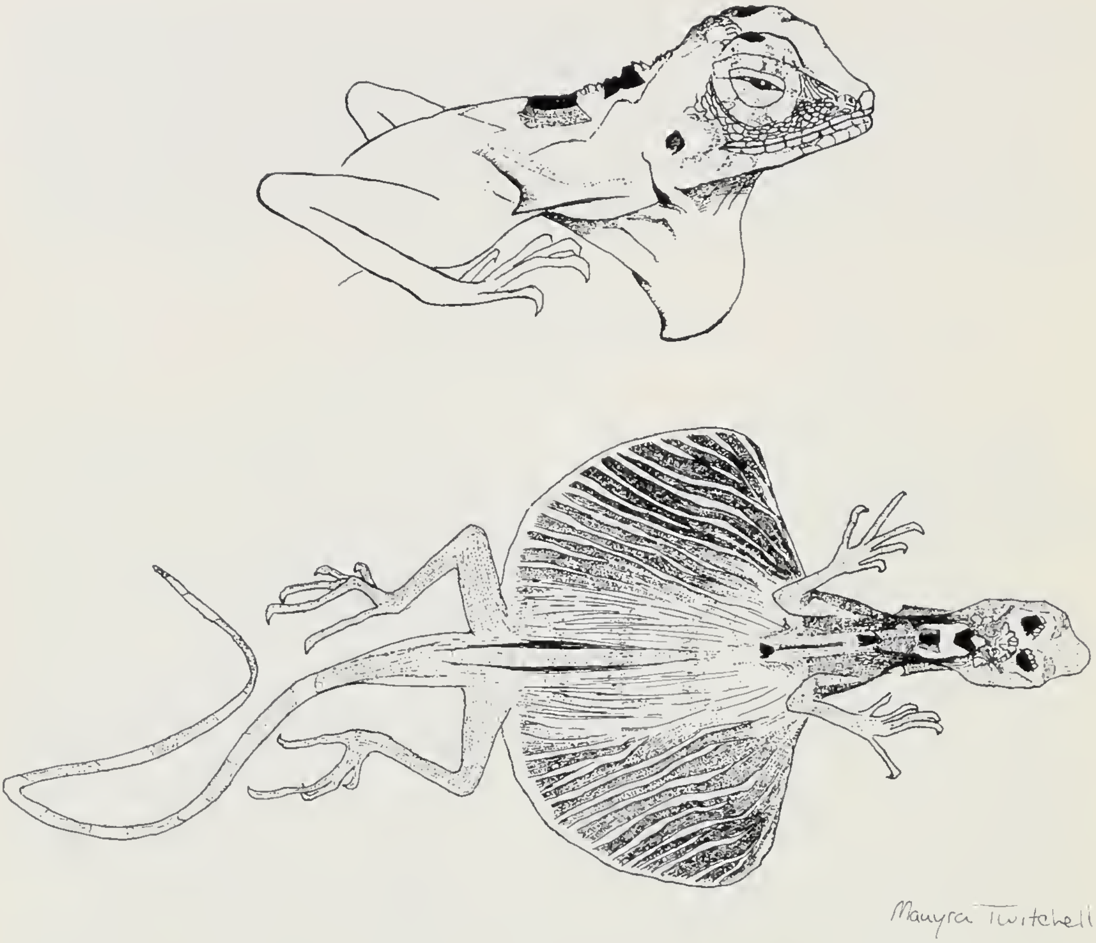

Figure 2. *Draco biaro* sp. nov., The type: MCZ 170898, from the island of Biaro, Sangihe Archipelago, Sulawesi Utara, Indonesia.

fan bears only small ones. The caudal scales are subequal; there is no caudal crest. A low nuchal crest consists of about 22 enlarged, tectiform middorsals. The adpressed hindlimb just reaches the forelimb insertion.

Teeth were not counted in this specimen because the number is inconsequential in relevant species and opening the mouth may entail damage.

In life the type was largely grey. There was a beige-tan wash on the cheeks and jowls where the pattern was of irregular mottling. There are two bold, sooty nuchal blotches; between and flanking these is strongly contrasting pale ash-grey, making a roughly H-shaped figure, viewed from above. The dorsum is irregularly banded with light and dark grey in a lichenate pattern. The chest was washed with dull yellow. The throat fan was pale lemon-yellow—almost white—with light grey barring. The dorsal surface of the patagium was sooty to slaty grey with a series of narrow ash-grey lines. The translucent, membranous skin of the flanks and ventral surfaces of the patagia looked light greenish with the patagia folded; this results from a pale bluish ventrolateral wash shading to pale yellow distally. When the patagia are expanded the dark dorsal color dominates, especially as sooty anterolateral blotches. The lappets were dull grey above, paler and yellowish grey below.

Variation. The sexes are quite similar. Six adult males measured 70 to 75 mm; seven adult females measured 71 to 75 mm; both sexes averaged 73 mm SVL. Eight of these 13 adults show some degree of supralabial carination. There may be low, somewhat irregular ridges (e.g., MCZ 170912, a male) or prominent, strong keels (e.g., MCZ 170910, a female).

I elected to quantify trunk scale size by the standard distance count method used in iguanid work (e.g., Lazell, 1972). In *Draco biaro* the middorsals are juxtaposed, subimbricate, and smooth, keeled, or weakly tectiform; there are 12–17 (average 15) in the standard distance. The ventrals are always sharply keeled and fairly well-aligned in transverse rows; there are 14–21 (average 16) in the standard distance.

There are 26–29 (average 28) subdigital lamellae on the fourth toe of the pes, distal to its separation from the third toe.

I could detect no sexual dimorphism in any mensurable or meristic characters.

Twenty specimens of *Draco biaro* have small scales, arranged in a whorl, over the tympanum. Two depart from this norm: MCZ 170899 has large scales over the tympanum. In MCZ 170919 the condition seems intermediate between a large scale and the thin, smooth skin of a typical tympanic membrane.

All specimens were very similar to the type in coloration in life. Females show little of the beige-tan wash on cheeks and jowls. Females have very small, unmarked grey throat fans, but the lappets are like those described for the male. The patagia of both sexes are similar. Juveniles tend to have a more strongly contrasting lichenate dorsal pattern in shades of grey than do large adults.

Inger and Musters concur that *Draco* of both the *lineatus* and *volans* complexes have four or five incisiform teeth. Musters subtracts two from the total between the caniforms to approximate real incisors while Inger gives the total count; I used Inger's method because I cannot readily see which teeth are actually socketed in the premaxillaries. I checked five paratypes of *Draco biaro,* MCZ 170913–17. Only MCZ 170914 lacks a median tooth or socket and really seems to have four teeth. MCZ 170917 has four teeth, one median, and one empty socket. MCZ 170915 has only three teeth, one median, and at least one empty socket. Five is probably the normal count for the species.

Comparisons. In the key provided by Musters (1983), *Draco biaro* goes to the *D. lineatus* complex. Both Musters and Inger (1983) agree that *D. volans* normally has six ribs in the patagium, a number not seen in any *D. biaro.* A close reading of both texts renders the case more equivocal, however. There seems to be no absolute distinction between these nominal, polytypic species. Diagnoses are compromised by the great variation exhibited within both the *lineatus* and *volans* assemblages.

In Table 1 I list some characters used by either Musters or Inger, or both, in diagnoses. My caveat is that many of the given character states are not absolute. Species recognition in *Draco* may well depend on finer grained analyses, including extensive knowledge of coloration in life, and field knowledge of ecology and behavior. This sort of knowledge helped Inger (1983: 8–15) separate *D. maximus* and *D. quinquefasciatus* at Nanga Telakit, Sarawak.

On 28–29 April, 1986, I collected two series of *Draco* near Batu Putih in northeastern Minahasa, Sulawesi Utara. This locality is about 36 km northeast of Manado, type-locality of *Draco lineatus spilonotus* (taxonomy agreed by all workers). Batu Putih is about 60 km south of Biaro. Field knowledge and fresh specimens from Minahasa made me sure I was seeing a new species on Biaro.

Because the Minahasa series differs from key characters given by Musters (1983:34), and because coloration in life is so rarely known (in proportion to its probable extreme value in species recognition), I provide a brief description of *D. l. spilonotus* here.

My series, MCZ 170922–933, includes five adult males, four adult females, and three juveniles. There is striking sexual dimorphism. The largest female is 72 mm (MCZ 170930), the larg-

Table 1. Seven ways in which species of *Draco* from Sulawesi differ.

	volans	*lineatus*	*biaro*
Ribs	6	5	5
Snout Y	yes	yes	no
Thorn	distinct	weak	absent
Postrostrals	4–6	5–7	8–10
Hindlimb	no	yes	yes
Tympanum	skin	scales	variable
Size	96	91	75

Ribs are those within and supporting the patagium. The snout Y is composed of continuous, enlarged, keeled scales. The thorn is an enlarged, pointed, anterior supraciliary. Postrostrals are the small scales in contact with the rostral, counting the first supralabials. The hindlimb is adpressed to determine if it is as long as the distance to the forelimb insertion ("yes") or not ("no"). The tympanum may be covered with undifferentiated small scales or smooth skin (see text). Size is maximum snout-vent length (SVL); the number is for a female in both *lineatus* and *volans*, but in *biaro* the sexes are equal. Size varies geographically in both wide-ranging species.

est male 64 mm (MCZ 170925) snout to vent. The male throat fan is relatively long, 96 to 102% (average 99) of head length; it is nearly triangular, gradually tapering, and acutely pointed.

The males are brilliantly colored. The entire head and neck region is boldly spotted and marbled with chartreuse, aquamarine, and copper-tarnish green on an olive-beige ground. On the trunk this ground color is marbled with grey. The patagia are bright salmon pink, orange, or orange-yellow. The belly is green. Both lappets and throat fan vary from brilliant lemon to sulfur yellow.

The females are darker and duller. The head and neck mottling is in shades of olive green and olive brown. The patagia are deep rich yellow or orange-yellow spotted or barred with near black. The lappets and throat are light yellow. Both sexes have some power of color change, to lighter or darker. This change does not seem to affect the patagia, lappets, or throat fan.

My specimens differ most notably from those described by Musters (1983) in patterning of the head and neck. They have retained their bold patterns in alcohol (three months at time of writing), though the bright colors have faded. The significance of the differences cannot be judged without far more extensive knowledge of populations in life.

I have examined six specimens of *Draco lineatus bimaculatus,* MCZ 26178–82 and 43640, from Mindanao. In these the rostral is tiny compared to that of *D. biaro.* The eye is roofed by large, plate-like, keeled supraciliaries. The enlarged, aligned, keeled scales on the frontal region form an arrow-shaped pattern, not a Y. There are 10 to 12 supralabials (60% have 11). A more cursory look at all other Philippines material in MCZ further convinces me that the relationships of *Draco biaro* do not lie with known *Draco* from that area.

On balance, the affinities of *D. biaro* seem to lie with the *lineatus* complex not the *volans* group. I predict the discovery of many more island forms in the Sangihe, Kawio, Nenusa, and Talaud archipelagos between Sulawesi and Mindanao.

Comments. Draco biaro is common on its small island, frequenting coconut palms and other smooth-barked trees. Most were encountered two to four meters from the ground and noosed with a long pole. Often they fled up the trunks and children climbed after them. They sometimes ascended more than 20 meters. Eventually, when pursued, they would launch and glide. Then one could observe two large, middle-aged men and several dozen children racing through the grass and brush after the flying lizard, which sometimes landed low enough to be caught by hand.

Courtship was often observed. The male rapidly extends the throat fan and lappets several times and then fans the patagia. Most adult females palpably contain eggs. Two eggs, MCZ 170920–21, were laid in a collecting bag with several females during the hours between capture and pickling. One egg was broken, but MCZ 170920 measures 14.7 by 7.8 mm. It is white and leathery.

Pulau Biaro is subtended to the south by at least one small coastal cay. Coconut palms and other trees grow on this cay, but I did not visit it. *Draco biaro* may occur there.

Six other species of reptiles were collected on Biaro on 4 April: the vine snake *Ahaetulla prasina,* the skinks *Mabuya multifasciata* and *Lamprolepis smaragdinus,* and three geckos. *Hemidactylus frenatus* and *Gehyra mutilata* are abundant Indo-Pacific human commensals. *Gymnodactylus jellesmae* is rare in collections and seems to have been previously known only from Sulawesi.

ACKNOWLEDGMENTS

I am indebted to Bernard Page, William Disher, Karen Phillipps, and Mark Hopkins, my companions in the field during most of our Indonesia expedition. Mark Hopkins took excellent color photographs of living *Draco lineatus* near Batu Putih. The people of Biaro, Minahasa, and the other areas we visited were enthusiastically hospitable and helpful. Franklin Ross curated and accessioned the material into MCZ in a most expeditious manner. Mauyra Twitchell contributed Figure 2, drawn from photographs by Greg Mayer. The entire expedition was funded by The Conservation Agency.

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NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. V. *ANOLIS DANIELI*, A NEW SPECIES OF THE *LATIFRONS* SPECIES GROUP AND A REASSESSMENT OF *ANOLIS APOLLINARIS* BOULENGER, 1919

Ernest E. Williams[1]

Abstract. A new giant anole, *Anolis danieli*, is described from northern and western Antioquia, Colombia. Formerly confused with *A. apollinaris* Boulenger, 1919, of Cundinamarca and southeastern Antioquia, the new species differs in the presence of a dewlap of moderate size in the female (absent in *A. apollinaris*) and in minor scale characters. *A. danieli*, *A. apollinaris* and *A. propinquus* Williams, 1984, are demonstrated to be a distinct subgroup within the *latifrons* species group defined by distinctly keeled head scales, relatively short limbs and a green ground color. Previous confusions regarding the taxonomic placement of *A. apollinaris* and *A. propinquus* are corrected.

INTRODUCTION

In 1970 I redescribed *Anolis apollinaris* Boulenger, 1919, primarily on the basis of a series of six specimens from San Pablo, Department of Cundinamarca, Colombia, in the Munich collection (ZSM 427–432) and the type specimen in the British Museum (BMNH 1946.13.22). I referred to the species' three additional specimens from Cundinamarca—two from Antioquia and one from Caldas. I compared the species only with *A. biporcatus* Wiegmann.

Material since made available to me from Cundinamarca and Antioquia now makes it quite clear that my 1970 material was composite, and that only the Cundinamarca specimens were *A. apollinaris*. Fortunately, the illustrations in Williams (1970) are of Munich specimens from Cundinamarca, which are true *A. apollinaris*. The specimens from Antioquia represent a new, although very closely related species. (The specimen from Caldas has not been re-examined.) Further, it can now be established that both *A. apollinaris* and the new species belong to the alpha section of the genus (Etheridge 1960) and must be referred to the *Anolis latifrons* species group (*sensu* Williams 1976); they are not at all close to *A. biporcatus,* which is a member of the beta section.

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Confusion as to the placement and affinities of *A. apollinaris* and as to the affinity or lack of affinity of the *biporcatus* and *latifrons* species groups has had a long history. Boulenger (1919) in his description of *A. apollinaris* expressed no opinion about its relationships. Burt and Burt (1931) referred a number of Colombian anoles to the species, but were quite wrong in their identifications as Dunn (1944) demonstrated. Dunn's own judgment was most importantly based on size (SVL of the type specimen of *A. apollinaris* 106 mm) and he compared the species with *A. solifer* and *A. copei* (both synonyms of *A. biporcatus*), which are approximately this size. Unfortunately, Dunn did not compare *apollinaris* with the other group of species, well known in western Colombia, that is comparable in size, in spite of the fact that he had previously reviewed this group—his "mainland giant anoles" (Dunn 1937).

Confusion of the *biporcatus* and *latifrons* species groups first occurred when Günther (1859), describing *Anolis fraseri,* included a specimen of *A. biporcatus* in the type series. Boulenger (1885) corrected the error at the species level, but apparently, as I have commented earlier (Williams 1966), still believed that the two taxa were close relatives. Dunn (1944) committed a parallel error in the reverse direction by associating *A. apollinaris* with the two synonyms of *A. biporcatus.*

In fact, none of the standard external characters used in anole taxonomy permit the placement of the *biporcatus* and *latifrons* species groups as widely separate taxa. Species characters are clear enough, but there is quite obviously marked convergence in ecomorphic features (*sensu* Williams 1972, 1983). The significant internal character of the caudal vertebrae—anteriorly pointing transverse processes on these vertebrae in the beta section of *Anolis* and the absence of these processes in the alpha section of the genus—was discovered by Etheridge (1960) only with the aid of X-rays.

This character was, of course, known to me in 1970, but by misfortune in 1970 no suitable X-ray equipment was conveniently available to me or to Etheridge (on whom I usually relied for assistance in this particular) nor were any dry skeletons available (there are still none). Therefore, I contented myself at that time with externals. Influenced by minor aspects of color pattern—green with some white spotting, which appeared to eliminate *A. fraseri* as a close relative—and by the short limbs, shared with *A. biporcatus* as well as *A. fraseri*, and quite unlike the long limbs of the *frenatus* subgroup of the *latifrons* assemblage, I accepted Dunn's (1944) allocation.

The recognition of a second species related to *A. apollinaris* and of the alpha affinities of both species began when two large *Anolis* from Antioquia belonging to the collections of the Museo de Historia Natural at the Colegio San José in Medellin (CSJ 111 and 168, now ICN 5997–98) were turned over to me by Stephen Ayala for examination. The female, CSJ 111 from Yarumal, had a very evident large dewlap and bore a paper label in Niceforo Maria's handwriting: "*Anolis purpurescens*." A caudal vertebra teased from its broken tail showed that it belonged to the alpha section of the genus, yet the scale counts routinely taken on *Anolis* specimens were disturbingly similar to those of *A. apollinaris.* The latter, however, was not only believed to be a beta anole, but, in the Munich series I had studied in 1970, five of the six were females, and they had shown at most a vestigial gular fold and not a dewlap.

The absence of transverse processes on the caudal vertebrae of the Yarumal female and in *A. apollinaris* was verified by X-ray. The two specimens from Antioquia attributed to *A. apollinaris* in 1970 were re-examined: MLS 81, recatalogued as MLS 926, a female, and AMNH 38725, a male. Marco Antonio Serna provided three additional specimens from Urrao, Antioquia, all males, from the Colegio San José collection.

For comparison with the specimens from Antioquia, new material of verified *A. apollinaris* has been required. Ten specimens collected by Juan Manuel Renjifo at Sasaima, Cundinamarca (INDERENA 2853–62) and two collected by José Vicente Rueda at Charalá, Santander (ICN 2865, 6017—a new record) have been available, as well as additional Cundinamarca specimens from the Museum of Comparative Zoology (MCZ) and the Instituto de Ciencias Naturales (ICN) in Bogotá. These comparisons fully established the distinctness of the Antioquian population, which may now be formally described as a new species to be named in honor of Hermano Daniel Gonzalez, now Director of the Museo de Historia Natural at the Instituto de La Salle, Bogotá, in recognition of his 37 years of association with the Colegio San José in Medellín, Antioquia:

Anolis danieli, new species

Holotype. ICN 5997 (formerly CSJ 111), adult male.

Type Locality. Urrao, Antioquia, Colombia. Collector and date of collection unknown.

Paratypes. Antioquia, Puerto Antioquia, Baja Rio Cauca: MLS 926, Hno. Ignacio Saza coll., January 1963. Sabanalarga: AMNH 38725, Hno. Niceforo Maria coll., no date. Urrao: MCZ 164894 (formerly CSJ 278), Marco A. Serna coll., 28 May 1972; CSJ 441, M. A. Serna and H. Echeverri coll., 23 March 1983; CSJ 720, M. A. Serna and H. Echeverri coll., 26 July 1985. Yarumal: ICN 5998 (formerly CSJ 168), collector and date of collection unknown.

Referred Specimen. "Western Colombia:" AMNH 4844, collector and date of collection unknown.

Diagnosis. A species very close to *A. apollinaris* but differing in the presence of a moderately large dewlap in the female (rather than a mere longitudinal fold indicating the position of such a structure), and in the possession of a differentiated anterior nasal (rather than a circumnasal separated from the rostral by a postrostral). Also, by having the keels in the frontal depression with keels oriented anteroposteriorly (rather than keels radiating from the center of the depression); by having a distinct parietal depression usually bounded by ridges (rather than a shallow depression never distinctly set off from the occiput); and by having the scales anterior and anterolateral to the interparietal subequal in size to those posterior to it, *except* for the scale row that abuts on the semicircles, which is abruptly larger (rather than *all* scales anterior and anterolateral to the interparietal markedly larger than those posterior to it).

Description. Head. Head scales moderate to small, rugose or obtusely to strongly keeled. Eight to 12 scales across the snout between the second canthals. A moderate frontal depression, the scales within it slightly smaller than the surrounding scales and with keels oriented anteroposteriorly (flat in MLS 926). Five to 8 scales border the rostral posteriorly. An anterior nasal scale differentiated (in ICN 5998, on one side, divided into upper and lower portions), in contact with the sulcus between rostral and first supralabial. About 7–8 scales between the supranasals dorsally.

Supraorbital semicircles separated by 3 scales, the middle one smallest, or (in AMNH 38725 and MLS 926) separated by 4 scales equal in size. Supraocular disk ill-defined but the medial scales longer and bluntly keeled, in contact with the supraorbitals or separated by one row of small scales. About 7 scales across the supraocular area between the supraorbitals and superciliaries. One to 3 elongate superciliaries anteriorly, flanked medially by moderately enlarged polygonal scales and continued posteriorly by granules. About 5–6 rather narrow canthal scales, the second largest, decreasing regularly in size forward. Five to 7 loreal rows, subequal or irregular in size.

Temporal scales granular. An indistinct double line of slightly enlarged intertemporal scales. Supratemporals increasing in size laterally toward the margins of the parietal depression. Interparietal round, slightly to much smaller than ear (indistinct or absent in MCZ 164894 and AMNH 4844). Two to 5 scales on each side between interparietal and semicircles. Three to 5 rows of scales behind interparietal larger than nape scales.

Suboculars separated from supralabials by 1 scale row or narrowly in contact. Seven to 9 supralabials to below the center of the eye.

Mental divided or nearly so, each half about as wide as long. Five to 8 scales behind the mental and between the infralabials. Two of these may be differentiated sublabials; if differentiated, as many as six moderately enlarged scales in sequence with the sublabials may be in contact with the infralabials. Central throat scales small, swollen, smooth or obtusely keeled, becoming gradually larger adjacent to the infralabials.

Dewlap. Large in male, extending onto first third of belly, nearly as large in female, extending past axilla. With crowded scale rows in both sexes, and scales on the skin between the rows; lateral scales irregular and weakly keeled in males, flatter and more regular in females; edge scales larger than ventrals and bluntly keeled in males, smooth and subequal to ventrals in females.

Trunk. Middorsals distinctly keeled, 0 to 4 rows slightly enlarged. Flank scales bluntly conical or pyramidal, separated, with each scale conspicuously surrounded by minute granules. Ventrals larger, squarish, subimbricate, smooth or slightly keeled.

Limbs. Upper arm scales swollen, unicarinate or smooth, surrounded by minute granules like the trunk scales. Lower arm scales more crowed, sometimes larger, imbricate and multicarinate. Thigh scales crowded, swollen, imbricate, unicarinate anteriorly, small, subconical, separated posteriorly. Tibial scales larger anteriorly, distinctly or weakly unicarinate, separated, posteriorly smooth, subimbricate. Supradigitals of hand and foot multicarinate. Twenty-three to 27 lamellae under phalanges ii and iii of fourth toe, pad rather narrow.

Tail. Long, about 3× snout–vent length, slender, slightly compressed, fragile, but breaks apparently not across vertebrae.

Size. The largest specimen of the type series is the male holotype (SVL 117 mm, tail length 331 mm). AMNH 4844 is a larger specimen (SVL 125 mm) but has not been made a paratype because it has an obscure dorsal pattern of broad transverse bands not seen in the type material and has only the inexact locality "western Colombia." The largest female, from Urrao, like the holotype, has an SVL of 104 mm. *A. apollinaris* may be a slightly smaller species. The largest male (INDERENA 2856) has an SVL of 112 mm, the largest female (MCZ 156308) 94 mm.

Color in Life. For most of the few specimens of *A. danieli* there is no data on color in life. The best information (translated) has been provided by Marco Antonio Serna for CSJ 820, a male:

> Back completely green with a few elongate spots of even brighter green dorsolaterally. A broad yellowish band extends from behind the eye to the dorsal crest, and a second band

> of similar color extends from behind the ear to a more posterior position on the dorsal crest. A yellowish white band above the forelegs. Pale yellow around the eye. Gular region yellowish green. Dewlap yellow with whitish scales. All the belly greenish yellow with a little blue ventrolaterally. Tail green with blackish bars. Palms of fore and hind feet whitish. Fore and hind legs green with barely perceptible bars of slightly darker green. At least twice during its life in captivity the animal changed to brown. When killed, it immediately began to change to rust brown.

This description may be compared with three descriptions of color in life for *A. apollinaris* that I have been able to obtain. W. W. Lamar reports for a female specimen from Sasaima, Cundinamarca:

> Top of head yellow green. Eyelids bright saffron yellow. A broad tan stripe continuous from neck to well down on tail where it is replaced by black bars. Side of head behind eye blue green to intense green. A pale greenish white line across upper labials to ear. Dewlap rather small and yellow green. Venter bluish green becoming more so distal to hind limb. A few poorly developed ocelli on sides of body.

Stephen Ayala, reporting on animals from the same general locality, gives the following details:

> *Anolis apollinaris* is a green lizard, with a prominent white line or zone under the eye between the snout and the sides of the neck. The green changes to dark brown in less than half a minute. Small white spots or thin diagonal lines may be seen on the sides of the female, and some females have a broad tan vertebral stripe covering the entire back and tail. Light brown, saddle-shaped spots or bands may appear across the back of the male (especially in the dark phase) and small or large blue or reddish spots occur on the shoulders or sides of the neck. The eyelids stand out because of their contrasting color: yellow in female and yellow orange in the male. The dewlap of the male is pale yellow green, with rows of green scales (brown scales in the dark phase).

For the animals from Charalá, Santander, a description by José Vicente Rueda is available (translated):

> Dorsally head and body *senf. green* (olive green), edge of supraobital semicircles and postparietals black. Middorsal body spot chestnut. Irregular symmetrical spots black with a bluish cast above the insertion of the forelegs. Symmetrical and irregular brown spots on the base of the hind legs. Tail with well-spaced transverse black bands. Sides: a white band extending from posterior supralabials to shoulder. Eyelids burnt yellow (rust yellow). Ventrally mental, gular, dewlap, chest and forelegs yellowish green. Belly, tail and hind legs chartreuse (cream yellow).

It is clear from these and other descriptions and slides that both species change color readily and show different elements of the pattern at different times. Both are predominantly green anoles, and it may not be easy to distinguish them on color alone.

Color in Preservation. Most of the few preserved *A. danieli* are dull dark gray-blue, lighter below, with obscure traces of cross bars middorsally and of light lines on the nape. The Yarumal female is a faded brown. Only AMNH 38725, the male from Sabanalarga, shows any distinctive pattern (well-depicted in Fig. 5). This specimen has mottled blue on the flanks, with the nuchal crest black, with faint and narrow yellowish cross streaks. The head is more brownish, mottled, the light patch on the labials whitish and the streak continuing it above the ear suffused with blue. The wider black streak parallel to this contains whitish spots as does the similar black streak in front of the shoulder. Between the two black streaks is an area that is grayish anteriorly, grading into a general darker coloration posteriorly. The posterior body, limbs and tail are essentially patternless, the tail more olive than blue. In general terms, but not in detail, this animal matches rather well the description of the color in life of CSJ 720 above.

A rather similar but distinguishably different head and nape coloration is seen in the most patterned of the preserved *A. apollinaris* that I have examined (ICN 2865, Fig. 6).

A. apollinaris, although the body patterns may often be somewhat obscure, shows even in preservative the patterns mentioned by Ayala: the saddle markings of males, the broad dorsal stripe, the small white spots ("ocelli" of Lamar) or thin diagonal lines of females. No such patterns have been seen in *A. danieli.* Even AMNH 38725—the most patterned of the small type series—shows no comparable patterns.

A. apollinaris, however, is now relatively well known, both in life and as museum specimens. *A. danieli,* as here described from only eight specimens, is still very inadequately understood. The relative absence of body pattern in *A. danieli* must for the present remain a poorly supported conclusion. AMNH 4844, which I have excluded from the type series and which has very imprecise locality, does show obscure broad banding.

In the Parque de Las Orquideas, the borders of which are only 15 km from Urrao, a population that in most respects is closely similar to *A. danieli* but is boldly patterned is known from a series of 5 specimens. It is, however, restricted to shaded forest. The body pattern, uniform in all specimens, of broad dark cross bands enclosing small light spots is quite unlike that of the most patterned known *A. danieli,* and the animals seem to have a slighter slenderer body build. I have provisionally excluded this series from the hypodigm of *A. danieli* as a distinct, though obviously sibling, species.

Ecology. Almost nothing is known of the ecology of *A. danieli.* CSJ 720 is reported from a garden within the city limits of Urrao, 1,850 m elevation. AMNH 38725 may be from a somewhat lower elevation (Sabanalarga, 1,250 m), while ICN 5998 from Yarumal is presumably higher (Yarumal, 2,265 m) Only MLS 996 from Puerto Antioquia may not be montane; Caceres near Puerto Antioquia is given as 85 m elevation, but sites above 1,000 m are relatively close by. Lack of precision in the older locality records makes any comment on altitudinal range at best tentative.

If *A. danieli* is like other members of the *latifrons* group, it should occur at low to moderate heights on large trees but not in canopy. *A. danieli*'s sibling, *A. apollinaris,* is known to behave in this fashion (observations by Juan Manuel Renjifo and student). *A danieli*'s occurrence in gardens indicates that it is not restricted to shaded forest, and *A. apollinaris* similarly occurs in rather open situations (J. M. Renjifo, personal observation). Stephen Ayala also reports that he has seen *A. apollinaris* in guava and several other trees in rural household "gardens" in areas of low forest in Cundinamarca, usually on the vertical trunks.

Distribution. A. danieli occurs in the northern regions of both the Western and Central Cordilleras in Antioquia. So far as is known, it is endemic to the Río Cauca drainage, extending from Puerto Antioquia and Yarumal in the north, to Sabanalarga and Urrao in the south; perhaps over a considerable range of elevations, but rather clearly montane. It is apparently replaced in the Western Cordillera in the Parque Nacional Natural "Las Orquideas" by the unnamed and more boldly patterned sibling mentioned above. To the east and southeast, it is represented by the species with which I previously confused it, *A. apollinaris.*

One juvenile but unmistakable *A. apollinaris* (CSJ 435) is known from El Retiro, 23 km southeast of Medellín in Antioquia. It is a female without a dewlap, with the anterior nasal separated by one scale from the rostral, and with the keels of the scales in the frontal depression radiating from the center. It has a distinctive pattern of diamond-shaped light rhombs on the middle of the back that matches perfectly the dorsal pattern of a juvenile *A. apollinaris* (MCZ 46422) from La Mesa, Cundinamarca.

The El Retiro specimen implies a close approach of these two closely related species, so similar structurally and not separated by any obvious physiographic or ecological barriers. What happens in the potential range of contact or overlap remains an open question.

Comparisons. Most of the characters of the species of the *latifrons* species group as I now understand it are summarized in Tables 1–3. I have added to the species in the group as listed by Savage and Talbot (1978) not only *A. apollinaris* (removed from the *biporcatus* species group of Williams 1970, 1976) but also *A. propinquus* Williams, 1984, described from a hatchling and in the description erroneously referred to the *punctatus* species group.

A. apollinaris, A. danieli and the still unnamed *danieli* sibling from the Parque Las Orquideas, along with *A. propinquus,* appear to constitute a distinct subgroup within the *latifrons* species group defined by distinctly keeled head scales, relatively short limbs, and a green ground color.

A. propinquus, on re-examination, seems clearly to belong here. Its size as a hatchling (41 mm SVL) implies a giant adult, and the lamellae number implies the same and fits well with counts found in the *latifrons* group. It lacks an interparietal—and this initially seemed significant—but absence of an interparietal occurs also, as an individual variation, in *A. danieli* (AMNH 4844; the interparietal is indistinct also in MCZ 164894) and in the Parque Las Orquideas sibling. Its dewlap or gular region was described in the field as "blue." From Lago Calima, Valle, it is geographically distant from other members of this subgroup. The radiating keels of the scales of the frontal depression and the nasal separated by one scale from the rostral suggest a closer relationship to *A. apollinaris* than to *A. danieli.* This unique specimen and the Parque Las Orquideas sibling indicate that there may be still further surprises within the *latifrons* group.

A. frenatus, A. purpurescens, A. latifrons, A. princeps, and *A. squamulatus* form a second subgroup. These species are relatively long-legged and share with *A. apollinaris* and *A. danieli* the character of green background coloration, but always have a dorsal pattern of oblique bands or rows of spots, sometimes also an ocellus in front of the shoulder. Despite considerable morphological variation in some features (most impressively in the swollen superciliaries of typical *A. latifrons*), this is a tight knit subgroup, in which, in fact, the separate species status of some nominal species—*A. purpurescens* and *A. princeps*—is still unconfirmed. (For this reason the latter species—cited by Savage and Talbot, 1978—were not mentioned in Williams 1976.)

A. fraseri is distinctive in head squamation—smooth head scales, the superciliaries squarish and *flat,* the suboculars always in contact with the supralabials. Its color—dark olive brown and green—is unlike that of any other species. It is short-legged like *A. danieli* and *A. apollinaris,* but it has more characters in common with the two Central American *latifrons* group endemics, *A. insignis* and *A. microtus* (not only short legs, but smooth head scales and suboculars in contact with supralabials and background coloration not green), and it is best grouped with these.

A. insignis and *A. microtus* may be, as Savage and Talbot (1978) suggest, relatives, but they are amply distinct from one another and, perhaps, end points of a former Central American radiation. *A. microtus* is the one *latifrons* group species, thus far described, that consistently lacks an interparietal scale.

ACKNOWLEDGMENTS

I am indebted to M. A. Serna and H. Echeverri for providing the newer specimens of *A. danieli,* to Dr. Charles Myers and to Dr. George Zug for the privilege of examining the specimens under their care, and to Dr. Pedro Ruiz and to Juan Renjifo for loan of comparative material of *A. apollinaris.* Dr. Stephen Ayala sent me the female from Yarumal that was the stimulus for the present investigation and has given much assistance and many essential comments. He has also generously donated the map that is here published as Figure 7. Laszlo Meszoely drew Figures 1–6.

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Table 1. *Latrifrons* group anoles with short legs and green bodies.

	apollinaris	*danieli*	*propinquus*
Head scales	keeled	keeled	keeled
Number between second canthals	8–12	8–12	12
Scales in frontal depression	with keels radiating from the center	with keels oriented anteroposteriorly	with keels radiating from center
Circumnasal/rostral	circumnasal or anterior nasal separated from rostral by one scale	anterior nasal in contact with sulcus between first supralabial and rostral	anterior nasal separated from rostral by one scale
Scales between supraorbital semicircles	2–4	3–4	3
Superciliaries	one very elongate scale followed by one or two shorter and these by subgranular series	one very elongate scale followed by two shorter and these by smaller conical scales	one extremely elongate scale (½ *supraciliary*) margin followed by granules
Ear	small	small	small
Loreal rows	5–7	5–7	7
Interparietal	small	small	not differentiated
Scales in parietal depression	large and rugose anterior to interparietal, smaller behind it	convex, weakly keeled or rugose, largest next supraorbitals, slightly smaller behind interparietal	small, subequal, weakly keeled
Scales between interparietal and semicircles	2–4	2–5	no interparietal
Scales between suboculars and supralabials	0–1	0–1	1

Table 1. Continued.

	apollinaris	*danieli*	*propinquus*
Supralabials to below center of eye	7–8	7–9	7
Trunk scales	swollen, keeled with interspersed granules; middorsals slightly enlarged or 2 rows distinctly so	swollen, keeled or pyramidal, *surrounded* by granules; 2–4 middorsal rows enlarged	granular, convex, subequal
Ventrals	smooth or keeled, juxtaposed to imbricate	smooth, subimbricate to imbricate	smooth, juxtaposed or subimbricate
Femoral scales	unicarinate, multicarinate near knee	unicarinate, multicarinate at knee	
4th toe lamellae	23–29	23–27	25
Dewlap	in male only	large in male and female; smaller in female	hatchling; no female known
Dewlap scales	densely scaled, scales bluntly keeled	densely scaled, keeled	scales crowded but a series of raised rows each two scales wide
Postanal scales	present in males, sometimes obscure; absent in females		
Scales posterior to vent	smooth or keeled	keeled	keeled
Tail crest	never present in any species		
Tail SVL	ca. 3×	ca. 3×	ca. 2×
Maximum SVL	♂ 112 ♀ 94	♂ 117 ♀ 104	unique type, a hatchling

Table 2. *Latifrons* group anoles with long legs and green bodies.

	frenatus	*purpurescens*	*squamulatus*	*latifrons*	*princeps*
Head scales	smooth or weakly keeled or rugose	nearly smooth	keeled	smooth, wrinkled or tuberculate	keeled
Number between second canthals	9–15	17	11–15	11–15	12–17
Scales in frontal depression	rugose, tubercular or keeled, keels without definite orientation	smooth	with keels anteroposteriorly oriented	wrinkled or tuberculate rather than keeled	nearly smooth
Circumnasal/rostral	circumnasal or anterior nasal separated from rostral by one scale	circumnasal separated from rostral by two scales	anterior nasal (sometimes divided) in contact with rostral	anterior nasal separated from rostral by one scale or (rarely) in contact	circumnasal or anterior nasal separated from rostral by one or two scales
Scales between supraorbital semicircles	2–5	2	3–5	3–5	2–6
Superciliaries	one very elongate scale followed by one shorter and this by subgranular series	one to two elongate scales followed by subgranular series	*ca. four relatively short scales* followed by subgranular series	*swollen, rugose,* boundaries indistinct, but anteriormost sometimes longer than wide but still short	one very elongate scale followed by subgranular scales

Table 2. Continued.

	frenatus	*purpurescens*	*squamulatus*	*latifrons*	*princeps*
Ear	large	moderate	large	large	large
Loreal rows	7–10	9	8–12	6–10	7–11
Interparietal	moderate	moderate/small	small	moderate	moderate
Scales in parietal depression	convex or tubercular, rather small all around interparietal	flat, nearly smooth, larger anterior to interparietal than behind it	convex, rugose, largest near surrounding ridges	flat, rugose, rather small all around interparietal	flat, nearly smooth, rather small all around interparietal
Scales between interparietal and semicircles	3–6	4	4–8	4–7	3–7
Scales between suboculars and supralabials	0–1	0	1	0–2	0–2
Supralabials to below center of eye	8–10	9	6–11	8–10	9–12
Trunk scales	keeled, subimbricate or juxtaposed, no enlarged middorsal rows	not swollen nor keeled, two middorsal rows slightly enlarged	swollen, keeled, juxtaposed with frequent interspersed granules	swollen, keeled or tuberculate, juxtaposed, middorsals not or slightly enlarged	swollen, keeled, juxtaposed, middorsals not enlarged

Table 2. Continued.

	frenatus	*purpurescens*	*squamulatus*	*latifrons*	*princeps*
Ventrals	smooth, juxtaposed to imbricate	smooth, juxtaposed	smooth or very weakly keeled, juxtaposed to imbricate	smooth, juxtaposed or subimbricate	smooth, juxtaposed to imbricate
Femoral scales	unicarinate, multicarinate at knee	—	unicarinate, multicarinate at knee	unicarinate, multicarinate at knee	unicarinate, multicarinate at knee
4th toe lamellae	22–28	22	22–27	21–26	22–25
Dewlap	large in males, poorly developed in females	unique type			large in both sexes
Dewlap scales	weakly scaled in crowded rows one scale wide	scales in rows 3 to 5 scales wide	in widely spaced rows each 3–4 scales wide	weakly scaled, scales not in distinct rows	weakly scaled, in rows 1–2 scales across
Postanal scales	present in males, sometimes obscure, absent in females				
Scales posterior to vent	smooth	smooth	keeled	smooth	smooth
Tail SVL	more than 2×		more than 2×	more than 2×	ca. 2×
Maximum SVL	♂ 137 mm ♀ 121 mm	juvenile	♂ 125 mm	♂ 124 mm ♀ 97 mm	♂ 121 mm ♀ 108 mm

Table 3. *Latifrons* group anoles with short legs and not green.

	fraseri	*insignis*	*microtus*
Head scales	smooth	smooth	smooth
Number between second canthals	6–10	7–12	7–9
Scales in frontal depression	smooth	smooth	smooth
Circumnasal/rostral	circumnasal or anterior nasal separated from rostral by one or two scales	circumnasal or anterior nasal separated from rostral by one or two scales	circumnasal separated from rostral by one scale
Scales between supraorbital semicircles	2–4	2–6	2
Superciliaries	no very elongate scale, the anteriormost scale short but longer than wide and followed by a double series of smooth series of smooth *squarish* scales	*3 short scales longer than wide followed by a series of smaller flat scales, irregular in size*	one scale longer than wide followed by smaller smooth or subgranular scales
Ear	moderate	moderate	moderate
Loreal rows	5–9	5–8	3–5
Interparietal	moderate	moderate	not differentiated
Scales in parietal depression	flat, smooth, large all around interparietal	flat, smooth all around interparietal	flat, smooth, moderately large all around interparietal
Scales between interparietal and semicircles	2–5	2–5	no interparietal
Scales between suboculars and supralabials	0	0	0
Supralabials to below center of eye	6–9	7–12	7–9

Table 3. Continued.

	fraseri	*insignis*	*microtus*
Trunk scales	smooth with interspersed granules, none or two middorsal rows enlarged	smooth, juxtaposed one to 3 middorsal rows enlarged	smooth or slightly rugose; flank scales rhomboidal; flat, middorsal scales elongate, rather irregular in shape
Ventrals	smooth or keeled, juxtaposed to imbricate	smooth, juxtaposed to subimbricate	smooth, juxtaposed or imbricate
Femoral scales	unicarinate, multicarinate at knee	smooth	wrinkled, not keeled
4th toe lamellae	18–24	23–27	20–22
Dewlap	large in both sexes	large in both sexes	large in both sexes
Dewlap scales	small, smooth	densely scaled, scales small, very weakly keeled	very weakly and densely scaled
Postanal scales	present in males, sometimes obscure, absent in females		
Scales posterior to vent	keeled	smooth	smooth
Tail crest	never present in any species		
Tail SVL	ca. 2×	ca. 2×	ca. 2×
Maximum SVL	♂ 116 ♀ 102	♂ 153 ♀ 135	♂ 111 ♀ 104

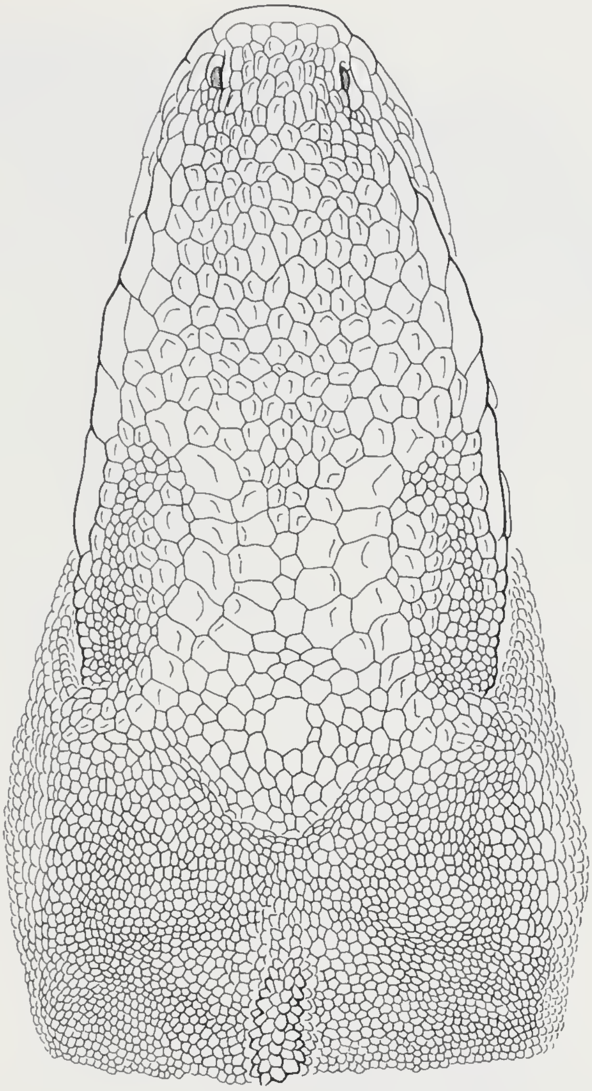

Figure 1. *Anolis danieli,* new species, ICN 5997 (holotype). Dorsal view of head.

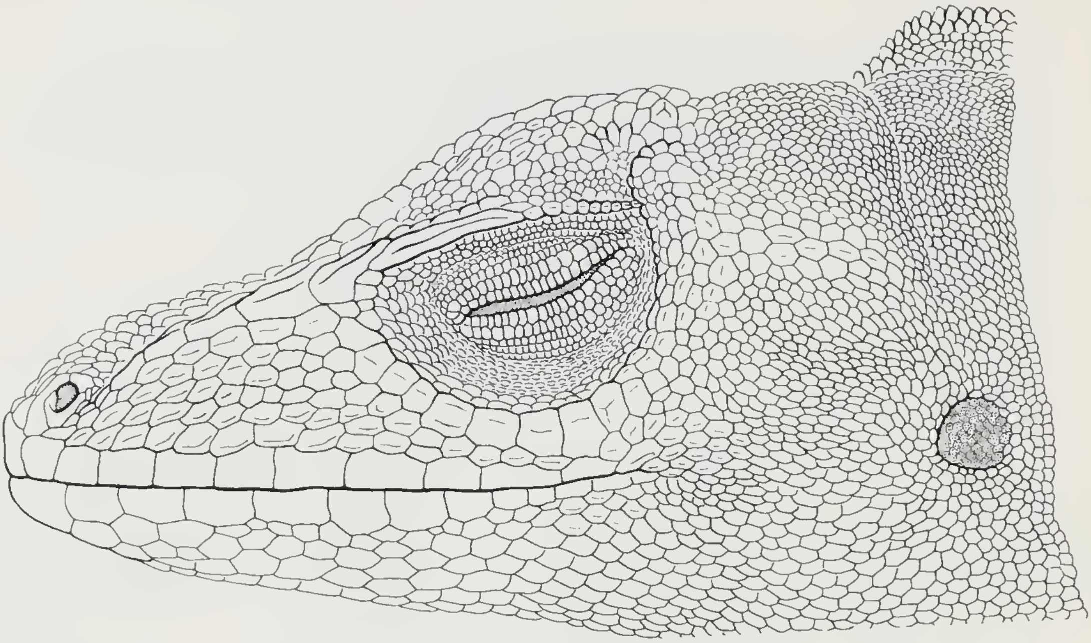

Figure 2. *Anolis danieli,* new species, ICN 5997 (holotype). Lateral view of head.

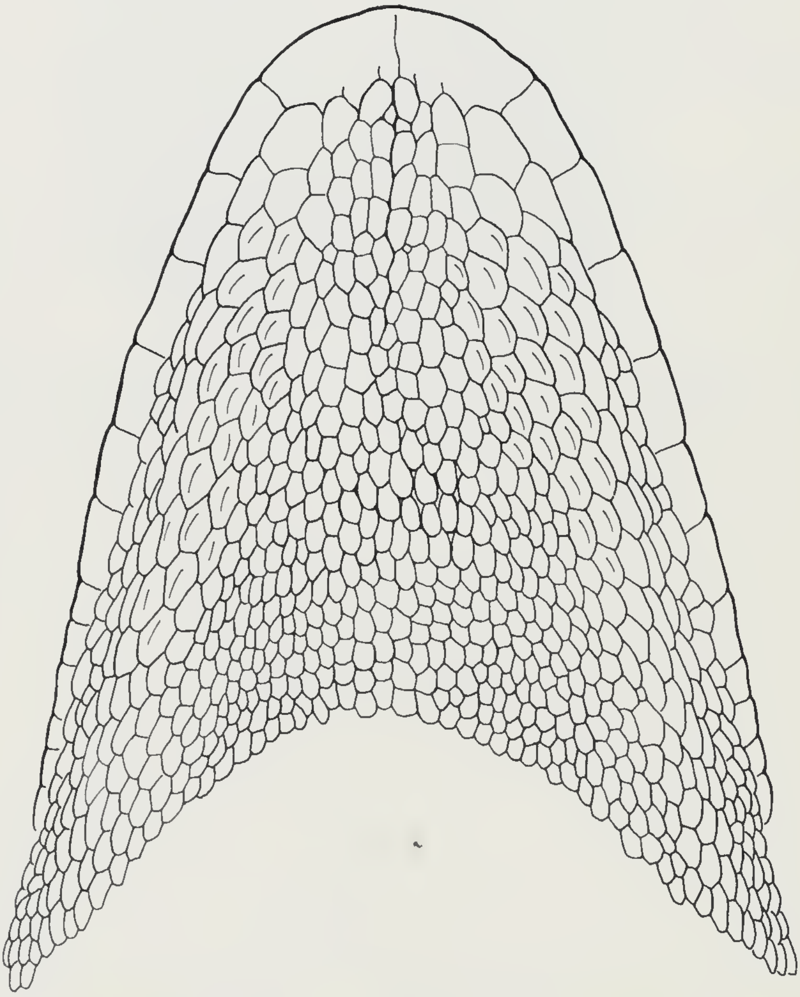

Figure 3. *Anolis danieli,* new species, ICN 5997 (holotype). Ventral view of head.

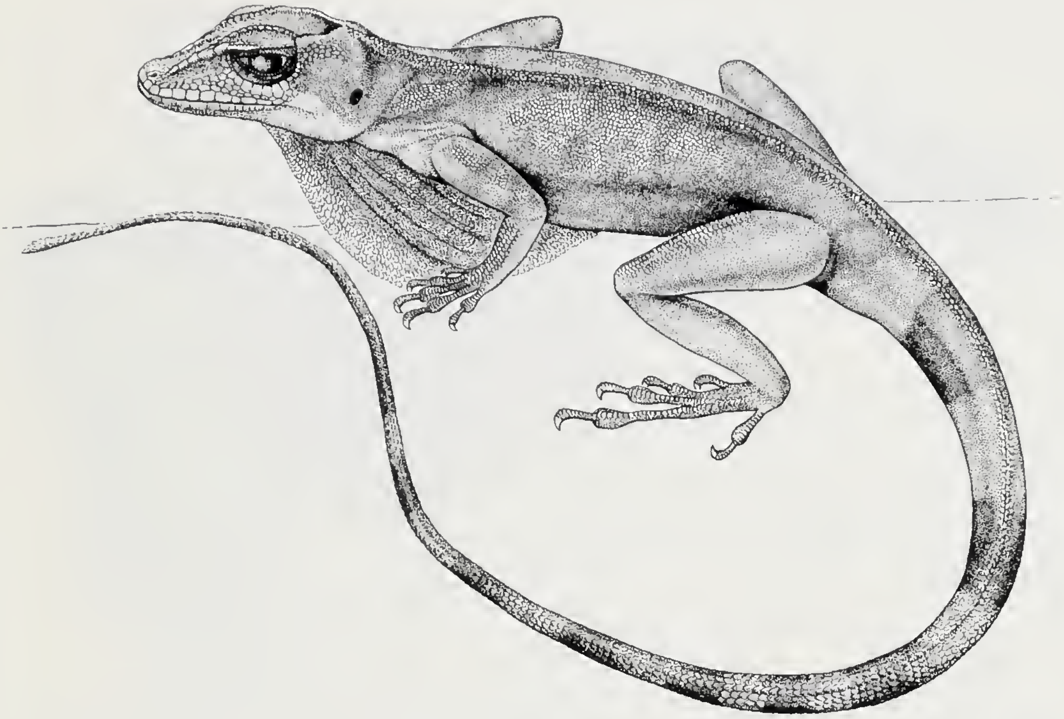

Figure 4. *Anolis danieli,* new species, ICN 5997 (holotype). Lateral view of whole animal.

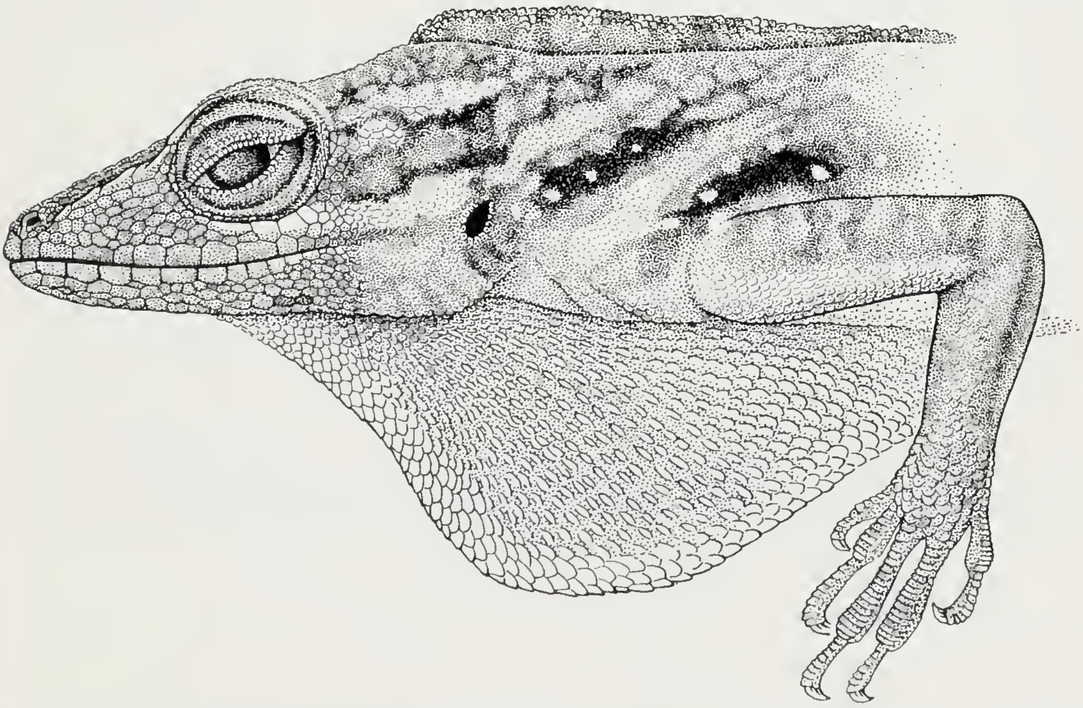

Figure 5. *Anolis danieli,* new species, AMNH 38725. The most distinct pattern seen in the type series.

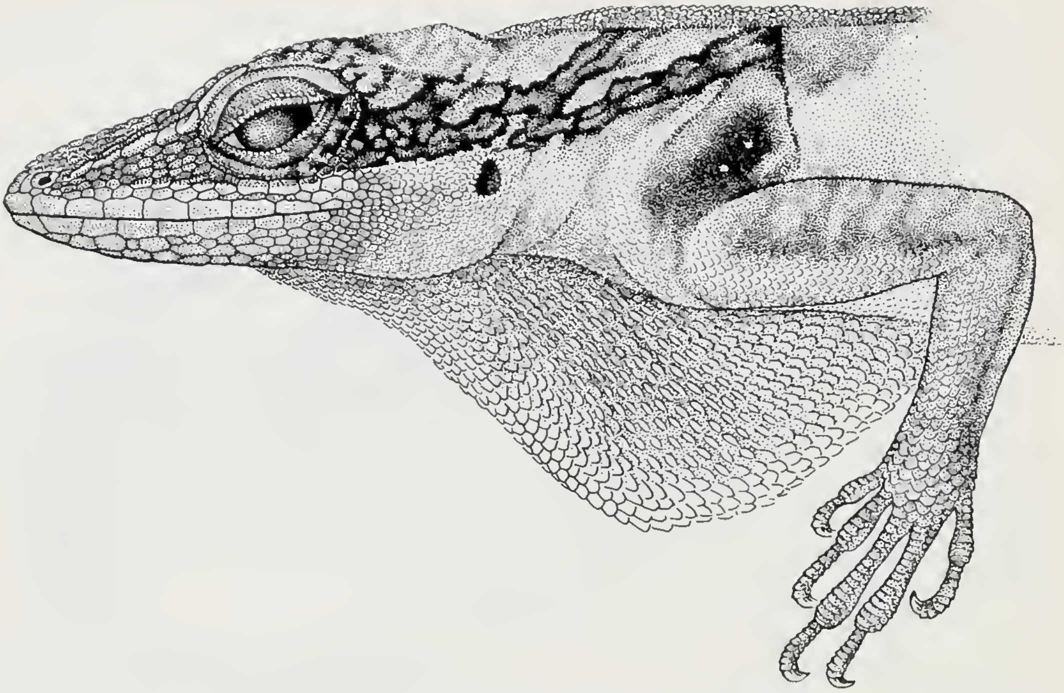

Figure 6. *Anolis apollinaris,* ICN 2865. The most distinct pattern seen in the specimens of this species examined.

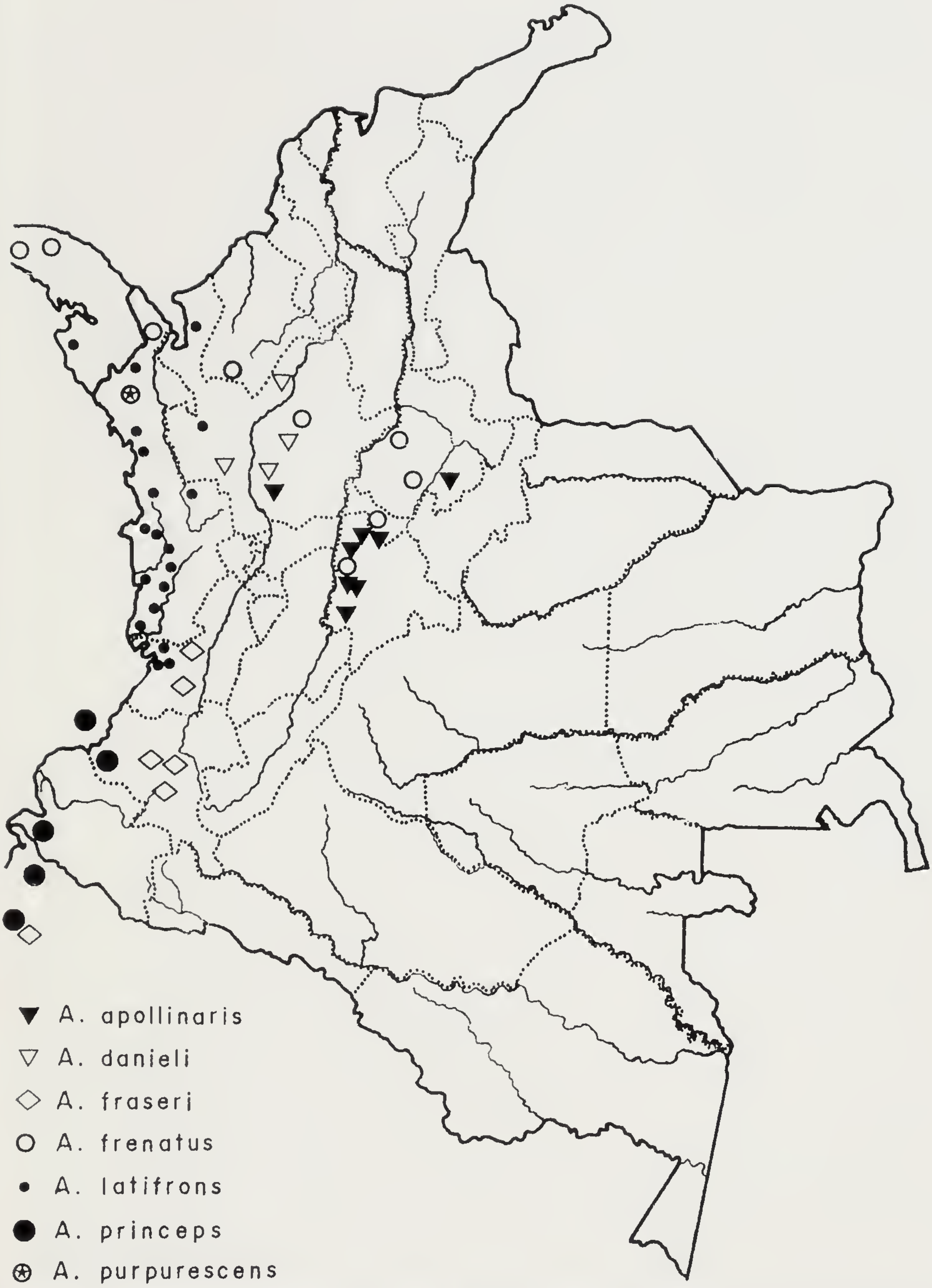
▼ A. apollinaris
▽ A. danieli
◇ A. fraseri
○ A. frenatus
• A. latifrons
● A. princeps
⊛ A. purpurescens

Figure 7. Map of distribution of the *Anolis latifrons* species group in Colombia.

BREVIORA

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NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. VI. TWO FUSCOAURATOID ANOLES FROM THE PACIFIC LOWLANDS, *A. MACULIVENTRIS* BOULENGER, 1898 AND *A. MEDEMI*, A NEW SPECIES FROM GORGONA ISLAND

Stephen C. Ayala[1] and Ernest E. Williams[2]

Abstract. *Anolis maculiventris* Boulenger, 1898, the widespread Pacific lowland *fuscoauratus* group anole of northwestern South America, is redescribed on the basis of a series of specimens from the region of the type locality in northern Ecuador. A second fuscoauratoid species, *Anolis medemi*, new species, is described from Gorgona Island, 56 km west of the Pacific Coast in Colombia.

INTRODUCTION

Anolis fuscoauratus-like lizards are widespread and often common at many sites in the Andean cordilleras and along the Pacific lowlands of northwestern South America. Williams (1976) recognized and briefly defined a fuscoauratoid complex as part of his key to the species groups of South American anoles. Nevertheless, accurate identification of individual specimens has often proved difficult: scale counts are very similar, distinctive colors fade soon after death, and only short descriptions of the type specimens of each species have been available for reference.

Williams (1976) listed five species in the fuscoauratoid group: *A. antonii* Boulenger, 1908, *A. fuscoauratus* Dorbigny, in Dumeril and Bibron, 1837, *A. maculiventris* Boulenger, 1898, *A. ortoni*

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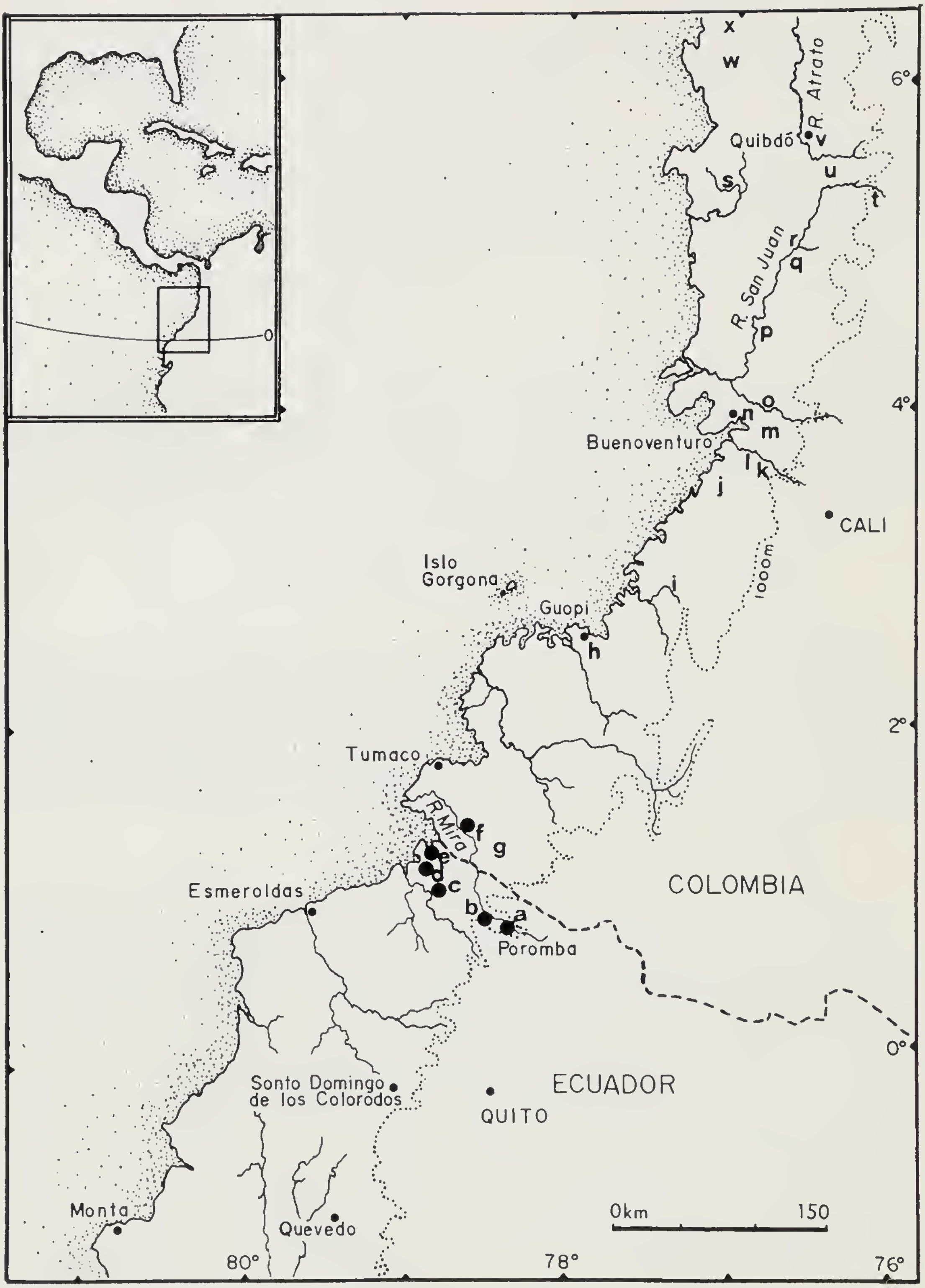
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Figure 1. *Anolis maculiventris* collection sites, and location of museum specimens: a–f, in the region of the type locality (a), specimens used for this description; g–x, other Colombian sites providing specimens assigned to this species. a—Hacienda Paramba, Imbabura (BMNH; NHMB, NHMW, ZMB); b—Lita, Imbabura (KU, NHMW); c—Cachabí, Esmeraldas (USNM), and Río Cachabí near

Cope, 1868, and *A. trachyderma* Cope, 1875. Two additional taxa, *A. tolimensis* Werner, 1916 and *A. mariarum* Barbour, 1932, were treated as synonyms of *A. antonii* but are now known to be valid species. *A. ortoni* has subsequently been considered a member of the *pentaprion* rather than the *fuscoauratus* species group because of its large, flat head scales and the low dorsal crest on its tail.

Fuscoauratoids are part of the beta section of the genus, with transverse processes on the tail vertebrae. Adults are small to medium size, reaching 50–60 mm snout–vent length. Their dorsal scales are small, uniform and usually keeled; belly scales are usually smooth, or sometimes bear a low keel; head scales are small and most often wrinkled or keeled, with those of the frontal depression sometimes much smaller than the others; the tail is round and slender, with no dorsal crest; toe lamellae are broad and well defined, totaling fewer than 20 on phalanges ii and iii of the longest hind toe.

An eventual definitive review of this group will require multivariate analysis, personal familiarity with each species' distinctive color patterns and behavior under natural conditions, and electrophoretic studies as well. Meanwhile, detailed knowledge of the characteristics and variation of the populations at each type locality (the topotypic populations) is essential for reliable identifications and comparison with lizards from other areas. We begin

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Río Basalito (USNM); d—Estación Forestal "La Chiquita," 14.4 km S. of Lan Lorenzo, Esmeraldas (MCZ); e—San Lorenzo, Esmeraldas (USNM); f—Tangareal, Nariño (ICN, MCZ, BMNH); g—La Guyacana, Nariño (FMNH); h—Guapi, Cauca (UVC); i—Quebrada Guanguí, Río Patia, upper Río Saija drainage, Cauca (AMNH); j—Río Raposo, Valle (UMMZ); k—Anchicayá, Valle, and various sites in the vicinity (ICN, IND-R); l—Llano Bajo, Valle, and Sabaletas (ICN); m—Hacienda Los Mangos, Río Dagua, Valle (BMNH); n—Buenaventura, Valle (BMNH, UMMZ); o—Granja Forestal Experimental, bajo Río Calima, Valle (BMNH, ICN, CSJ, KU); p—Quebrada Docordó, between Cucurrupí and Noanamá, Chocó (AMNH); q—Peña Lisa, Condoto, Chocó (BMNH, MCZ, ICN); r—Andagoya, Chocó (BMNH, USNM, ICN); s—Río Dubasa, Chocó (MCZ); t—Pueblo Rico, "Caldas," now Risaralda (BMNH); u—area between Río San Juan and Río Atrato (LACM); v—Quibdó, Chocó (CSJ, ICN); w—Alto del Buey, Chocó (LACM); x—Serranía del Baudo, Chocó (LACM). A list of the museums mentioned is in the acknowledgments.

here a series providing more useful descriptions, comparisons of the named tax within the *fuscoauratus* group, and descriptions of some new species found during our work. Redescriptions of named species are based mainly on specimens recently collected at or near the type localities. Montane fuscoauratoids are discussed in a following report.

The map (Fig. 1) includes an additional 16 Colombian localities for *A. maculiventris,* including six localities (93 specimens) visited by Ayala's group, and 10 based on specimens in various museums. The term "large adult" refers to our estimate of modal large adult size, based on snout–vent length (SVL) measurements. It may exclude the occasional very large individual and does not take into account sexual size differences mentioned in the text. Most measurements used were made at the time of preservation (e.g., all specimens collected by one of us (SCA) or Ayala's collaborators in Colombia), but some were taken after different times in preservative. Ayala has seldom found more than a 2-mm shrinkage following preservation for anoles that measured 50–55 mm in life.

Anolis maculiventris Boulenger, 1898

Syntypes. BMNH 1946.8.13.33, an adult male (SVL 45 mm), BMNH 1946.8.13.34, an adult female (SVL 50 mm), Hacienda Paramba, Imbabura, Ecuador (0°49′N, 78°21′W), W. F. H. Rosenberg and assistants coll.

This is a small brown lizard, the only fuscoauratoid yet described from the western lowlands of Ecuador and central and southern Colombia (Fig. 1). Its type locality was cited as Hacienda Paramba, a farm in the Mira River valley between Ipiales and San Lorenzo in northern Ecuador. Río Mira briefly forms part of the Colombia-Ecuador border not far below the farm. The two *maculiventris* syntypes were donated to the British Museum by W. F. H. Rosenberg, who together with various assistants collected extensively up and down the valley between 1896–1899. Rosenberg was a collector-dealer, who frequently had some of his specimens first determined and described by Boulenger, and then sold the remainder of his series to other museums. Rosenberg's *maculiventris* must have come from the lower elevation, wet forested regions downstream (0°50–53′N, 78°20–30′W), possibly in the Province of Imbabura (south bank of the Río Mira at Paramba), or Carchi (north bank of the river at Paramba), or perhaps even in Esmeraldas (20 km below the farmhouse). Upstream, the valley becomes an arid, almost treeless desert (tropical and premontane thorn woodland, in the Holdridge classification), unsuitable for forest lizards like *A. maculiventris.*

The following description is based on our study of the two British Museum syntypes, plus 13 additional *maculiventris* from nearby sites in Imbabura, Esmeraldas and Nariño (Figs. 1a–f). COLOMBIA. *Nariño.* Tangareal, along the Río Mira: MCZ 159587–89, 160216. ECUADOR. *Esmeraldas.* Immediate vicinity of Cachabi: USNM 234723; Río Cachabí near Río Basalito: USNM 234724; San Lorenzo: USNM 234725; Estación Forestal "La Chiquita," 14.4 km S. San Lorenzo: MCZ 160248. *Imbabura.* Lita, 520 m: KU 133437, NHMW 12809; Paramba: BMNH 1946.8.13.33–34 (syntypes), NHMB 5060, NHMW 12810–11, ZMB 16462 (the latter four specimens are probably Rosenberg material seen by Boulenger). Scale counts for the male and female syntypes, respectively, are given in parentheses.

Description. Head. Head scales moderate to small, smooth, tuberculate or weakly keeled. Ten to 14 (m: 11, f: 14) across snout between second canthals. Frontal depression distinct, the scales within it posteriorly minute and tubercular, anteriorly slightly larger, smooth and flat. Six to nine (m: 8, f: 9) postrostrals, including the two anterior nasals. Anterior nasal in contact with the sulcus between rostral and first supralabial, rarely divided horizontally.

Supraorbital semicircles well defined, separated by three or four (m: 3, f: 4) small scales, separated by circumorbitals from the scales of the supraocular disk. Supraocular disk rather well defined, 5–10 enlarged scales, usually 1–3 much larger than the others, smooth or weakly keeled, grading laterally, anteriorly and posteriorly into granules. One elongate superciliary covers about one-third of the superciliary border, followed by one or two much shorter scales and then by granules. Canthal ridge distinct, canthals about nine, first 4–5 larger, the anteriormost in contact with the first supralabial or separated by one scale. Six to nine (m: 8, f: 8) loreal rows, the one or two lowest largest. Temporals and supratemporals granular. No distinct intertemporal zone or line of enlarged scales. Supratemporals grading into slightly larger scales lateral and anterior to the interparietal. Interparietal with well defined parietal eye, smaller, much smaller than or subequal to ear. Surrounding scales smooth, flat, pavement-like, much smaller than interparietal. Four to nine (m: 7, f: 9) scales between interparietal and semicircles. Scales behind interparietal tiny rounded granules, not or hardly differentiated from nape granules.

Subocular in contact with supralabials. Six to nine (m: 8, f: 7–8) supralabials to below the center of eye.

Mental almost completely divided, in contact with seven to ten (m: 9, f: 8) scales between the infralabials. No differentiated sublabials.

Trunk. Dorsal scales subgranular, smooth or weakly keeled, subequal or two median rows very slightly enlarged. Ventrals larger than dorsals, smooth, flat or slightly swollen, separated, juxtaposed or subimbricate. Chest scales in female smooth (poorly visible in male because of dewlap).

Dewlap. Extending well beyond insertion of forelimbs in males, absent in females. Lateral scales in rows separated by naked skin. Edge scales smooth, no larger than lateral scales.

Limbs. Limb scales unicarinate anteriorly, granular behind. Supradigitals multicarinate. Twelve to 16 (m: 15, f: 16) scales under phalanges ii and iii of fourth toe.

Tail. Round or slightly compressed, never with a crest, about 2 × snout–vent length. Enlarged postanals almost always absent, but visible in occasional males.

Measurements. Five males in this series measure 43–46 mm SVL (m: 43, Boulenger gave 45); six females measure 44–49 mm (f: 49, Boulenger gave 50). Based on our series of nearly 100 Colombian *maculiventris* >40 mm SVL, most large adults measure 45–48 mm, with exceptional specimens reaching 50 mm, and with no apparent sexual difference. Tail almost twice snout–vent length.

Color. Information on the color in life is available for only one of these specimens, KU 133437, a male from Lita, Imbabura—S. R. Edwards: "By night, sleeping on a leaf. Dorsum light brown. Dewlap orange peripherally, red medially. Venter tan. Tail barred, tan and grayish brown." Other specimens assigned to this species from sites farther south include MCZ 160249, a male from Tinalandia, Pichincha, 16 km from Santo Domingo de los Colorados on the road to Quito—K. Miyata:

> Collected at night. Color light brown with hint of olive. Dark brown markings. Can change quickly to dark mahogany brown with almost black look. Dark brown line between eyes over top of head. Venter pale dirty brown, yellowish around cloaca. Dewlap bicolored, dull orange around edge, dirty brick red along throat. Scales on dewlap yellow anteriorly, dirty white posteriorly. Iris brown.

KU 133709, a female from 4 km N. of Quevedo, Los Rios—T. H. Fritts:

> At base of elephant ear plant at edge of stream by day. Dorsum olive brown with few black flecks; venter gray-beige invaded laterally by olive brown flecks of lateral body.

And a composite description drawn from several dozen specimens from the region to the north around Buenaventura, Valle:

> A brown or gray-brown lizard, most often patternless or sometimes with diagonal series of small yellow spots on the sides, or occasionally in males with vague dark shadows or bands between the pale rows of spots. When frightened it can turn much darker, especially on the back and head. Some females have a striking pale tan or yellow vertebral stripe with dark borders. A dark interocular bar may sometimes be present. Both sexes often have a small but distinctive black spot on the back of the head. In occasional specimens several other less well-defined spots extend as a series along the back. The belly is pale tan or gray-white, speckled along the sides with brown spots. The gular region is white, yellow-white or sometimes pale yellow-green; in males the underside of the tail is yellowish. The male dewlap is reddish pink behind the brick red anteriorly, with longitudinal rows of white scales, and the tail has wide light and dark brown bands.

Distribution. Anolis maculiventris ranges along the wet Pacific lowlands between central Ecuador and central Colombia (Fig. 1).

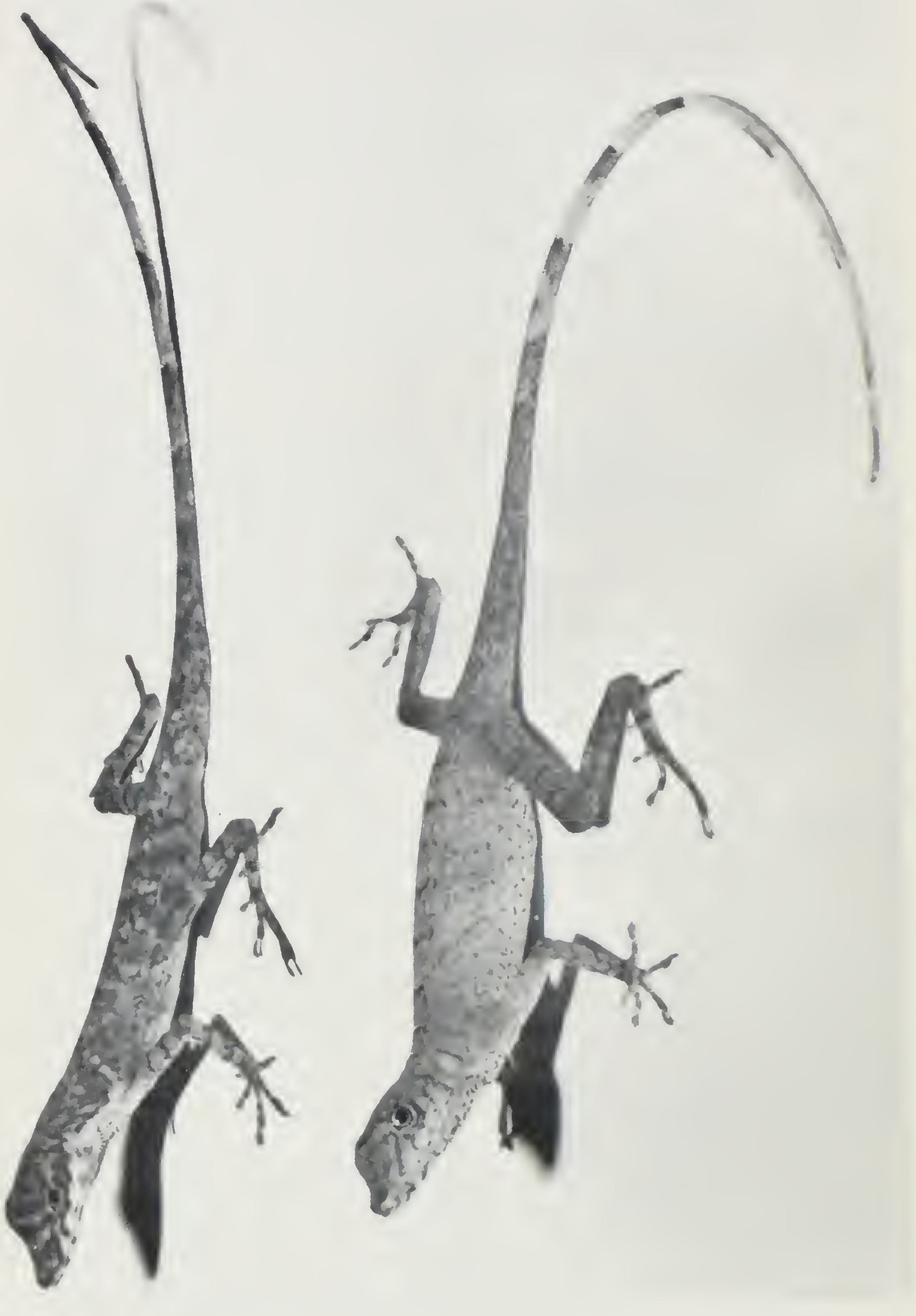

Figure 2. *Anolis medemi* from Gorgona Island: male above, female below.

Status of the members of the fuscoauratoid complex farther north remains unresolved, perhaps involving other undescribed taxa. Whether the Central American fuscoauratoid *A. limifrons* enters Colombia from the Panamanian Darien is uncertain. Dr. Charles Myers is examining populations from that region.

A second western fuscoauratoid anole from Gorgona and Gorgonilla Islands, 56 km off the Colombian Pacific Coast, is described here as a distinct species, closely related to *A. maculiventris.* The earliest specimen we know of was collected in 1938. The species was discussed and illustrated, but not named, in a preliminary treatment of Gorgona Island lizards (Ayala *et al.* 1979: 234–5, figs. 16, 17).

Anolis medemi, new species

Holotype. ICN 4371, adult male, Isla Gorgona (2°59′N, 76°12′W), La Esperanza, Cauca, Colombia. Stephen C. Ayala coll., 22 May 1979.

Paratypes (22). COLOMBIA. *Cauca.* Isla Gorgona: SDNHM 31122: C. S. Perkins coll., 22 February 1938. MCZ 78944–48: Federico Medem coll., 1961. MCZ 168519: Humberto Carvajal coll., 4 April 1977. IND-R-0468: Inge E. Morales, C. Chaparro and Pedro Rodriguez coll., 21 May 1978. IND-R-2226: Humberto Carvajal coll., 21 May 1979. IND-R-2899: Juan Manuel Renjifo coll. MCZ 168520–22: Humberto and Fanny Carvajal coll., 26 May 1979. CSJ 690: Henry von Prahl coll., 26 May 1979. ICN 4364–65, 4367–71, S. C. Ayala, H. Carvajal and F. Carvajal coll., 19–24 May 1979. Isla Gorgonilla: ICN 4366: Olga Castaño coll., 22 May 1979.

Diagnosis. A beta *Anolis* of the *fuscoauratus* species group, most closely related to *A. maculiventris* but slightly larger, with an overall orange-brown color (rather than olive or gray-brown) including a well-defined pattern of darker brown bars and spots on the back and sides.

Description. (Information on holotype in parentheses.) *Head.* Head scales moderate to small, weakly keeled or smooth. Snout moderately short, 9–15 (15) scales across snout between second canthals. Frontal depression moderately deep and well defined, scales within minute, granular, much smaller than surrounding scales, 7–10 (10) across. Five to eight (7) border rostral posteriorly. Anterior nasal in contact with rostral and rostral-first supralabial sulcus. Eight scales between supranasals dorsally.

Supraorbital semicircles well defined, separated by two or three (3) small scales, separated from supraocular disk by one or two rows of circumorbitals. Supraocular disk moderately well defined, 5–11 (8) enlarged scales, usually 1–3 larger than others, smooth or weakly keeled, grading laterally and posteriorly into granules, anterolaterally into moderately large scales, posterolateral area minute granules. One elongate superciliary extends over anterior half superciliary border, followed by 0–2 (1) shorter scales and then by granules. Canthus distinct posteriorly, less defined anteriorly, 8–10, usually 9 (10) scales to below nostril, first and second largest, anteriormost contacting first supralabial scale. Six to nine (9) loreal rows, lowermost largest. Temporals and supratemporals granular, intertemporal area not distinctly differentiated. Supratemporals grading into slightly larger scales around interparietal. Parietal eye clearly defined. Interparietal elliptical, smaller than or subequal to oval ear. Surrounding scales smooth, flat or swollen, much smaller than interparietal. Three to eight (7) scales between interparietal and semicircles, 3–5 between interparietal and smaller rounded granules on nape.

Suboculars in contact with supralabials. Six to nine (8) supralabials to center of eye. Mental almost completely divided, in contact with six to nine (8) scales between infralabials; these scales larger laterally, but no differentiated sublabial rows.

Trunk. Dorsal scales small, granular, weakly keeled, subequal or two to four median rows very slightly enlarged. Ventrals 4–5× larger than dorsals, smooth, rounded, separate, juxtaposed or slightly subimbricate. Chest scales in female unkeeled (poorly visible in male because of dewlap).

Dewlap. Extending onto anterior one-third of belly in males, absent in females. Lateral scales in well-spaced longitudinal rows, larger than ventrals; edge scales smooth, subequal to or slightly smaller than lateral scales.

Limbs. Limb scales unicarinate dorsally and anteriorly, granular behind. Supradigitals multicarinate. Thirteen to sixteen (15) lamellae under phalanges ii and iii of fourth toe.

Tail. Round or slightly compressed, slender, with no crest,

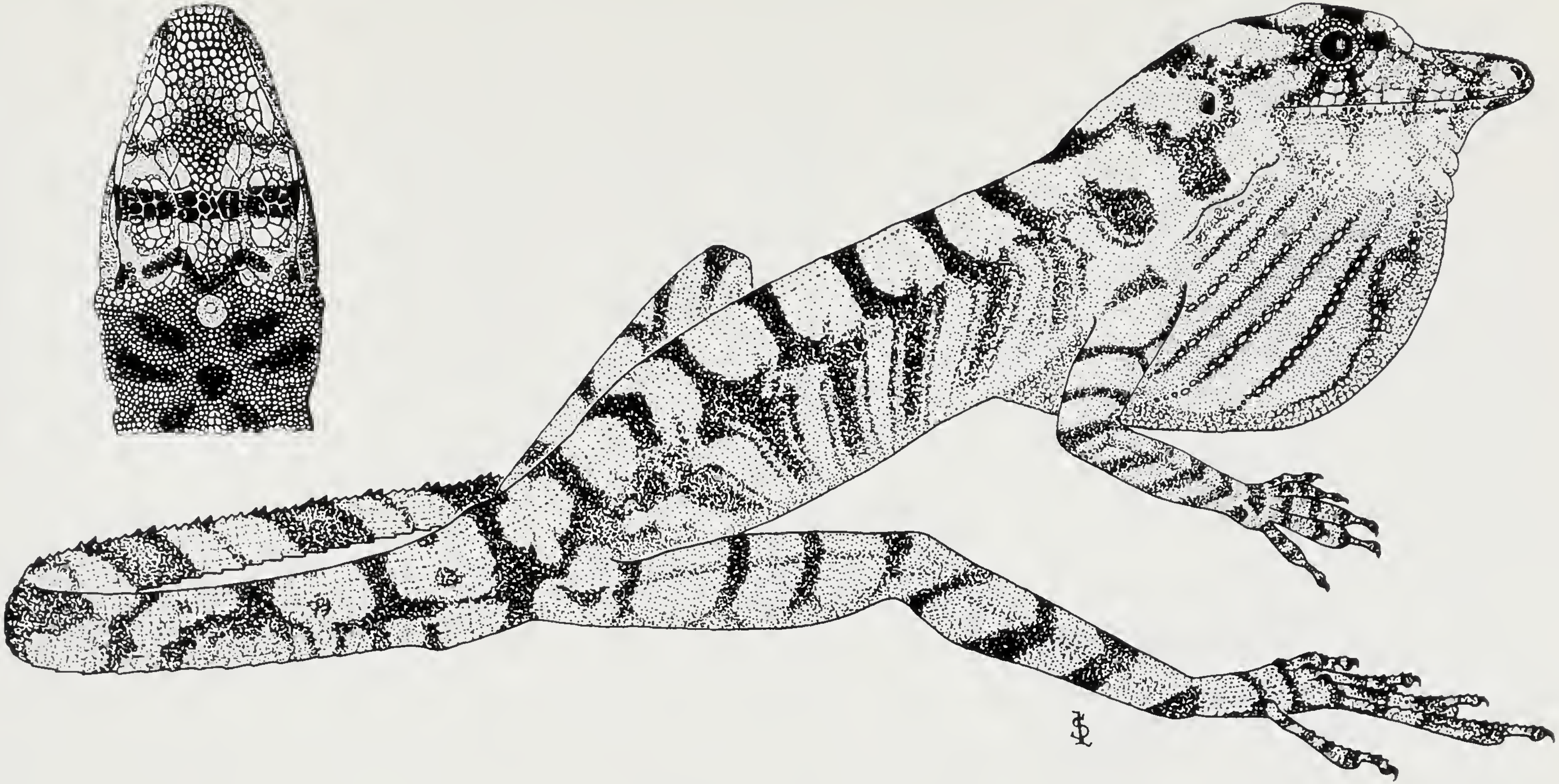

Figure 3. James Lazell's drawing of MCZ 78944 shows the boldly accentuated pattern of the series preserved by Federico Medem.

about 2× snout–vent length. No enlarged postanal scales (except in MCZ 78947).

Measurements. Holotype. Head length 15 mm, head width 7.0, snout–vent length 46, tail 83, foreleg 21, hindleg 37, reaching between eye and ear. Large adults 49–51 (largest of 20, 52 mm) SVL, with a 90–95 mm tail.

Color. Color in life brown with a definite orange cast. Most individuals show some evidence of darker brown bands or bars across body, legs and tail. Those that, like the holotype, are more prominently marked have 9–11 dark brown spots or crossbars along the back, 5–6 becoming vertical or diagonal dark brown bands on flanks, separated by pale yellow-brown zones, lines or spots; in others, darker brown pattern limited to vertebral region. Pale zones toward end of tail sometimes very light tan or even almost white, accentuating contrast with darker brown bands. Several specimens have dark lines radiating forward, upward and back from eye region, and a dark brown supraocular crossbar. Occasional females show sex-linked vertebral stripe morph seen in females of many other anoles; here stripe golden yellow with dark brown edges. Clearly defined occipital spot behind parietal eye; round, dark brown and almost always present even when remaining pattern scarcely visible. Belly pale tan or gray-white, sometimes with tiny brown flecks toward sides. Dewlap new-brick reddish orange, brighter anteriorly, with 5–6 longitudinal lines of yellow scales.

Background color of five paratypes collected by Federico Medem considerably faded, leaving darker pattern curiously accentuated, almost white with bold brown bars (Fig. 3). Most other preserved specimens similarly patterned, but pattern blends slightly, or almost completely in some females, into characteristic orange-brown background color.

Etymology. This lizard is named in memory of Dr. Federico Medem, who first brought this species to our attention, and who was director for many years of the Villavicencio Field Station of the Universidad Nacional de Colombia.

Comparisons. Anolis medemi is easily distinguished from the other three anoles known to occur on Gorgona Island: *A. princeps* Boulenger (some authors have cited it as *A. latifrons*) is much larger and green with brown diagonal stripes on the sides; *A. biporcatus* (Wiegmann) is larger, more robust and usually uniform

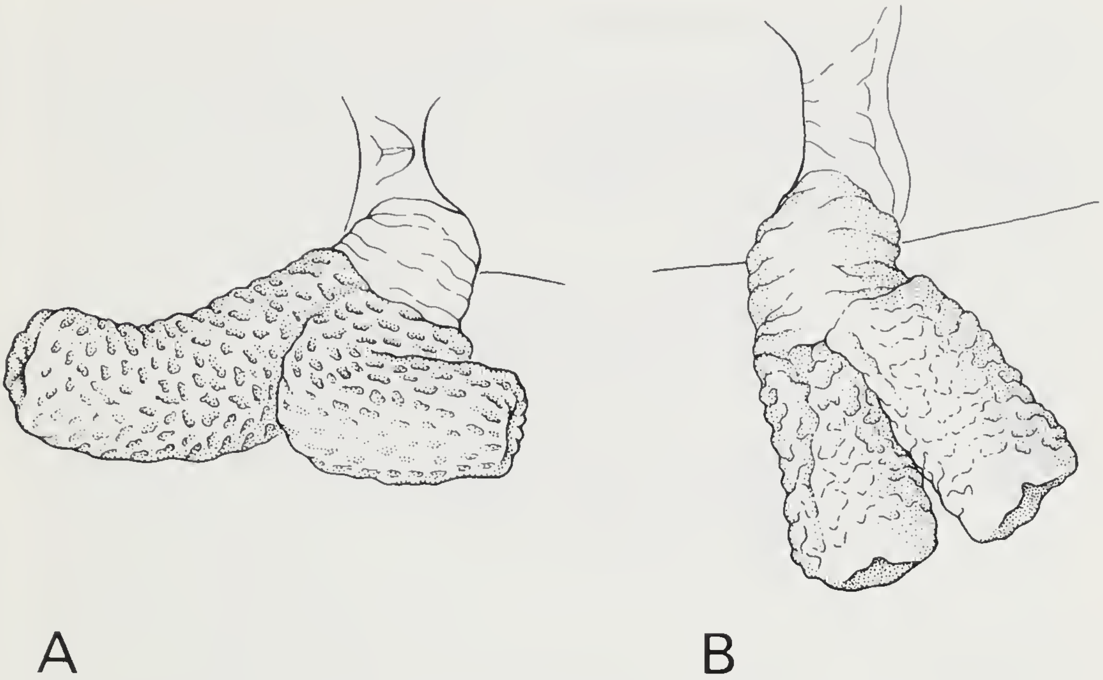

Figure 4. Hemipenes: A. *Anolis medemi.* B. *Anolis maculiventris.*

green—the regional race *A. biporcatus parvauritus* Williams may prove to be a distinct species; and *A. chloris gorgonae* Barbour (variously cited as *A. chloris* or *A. gorgonae*) is a sky-blue insular race of the common green mainland species *A. chloris* Boulenger.

Parker (1926) listed two additional anoles from Gorgona Island whose presence there remains unconfirmed. His two specimens unfortunately seem to have been misplaced while in one of the authors' (SCA) care: BMNH 1926.1.20.106, listed originally as *A. "fasciatus,"* is a juvenile *A. chocorum* Williams and Duellman, a rain forest species found sporadically between Costa Rica and western Colombia; BMNH 1926.1.20.107, listed as *A. "lemniscatus,"* appears indistinguishable from specimens of *A. tropidogaster,* a bush and grassland anole found in Panama and northern Colombia. Peters and Donoso-Barros' (1970: 48) undocumented mention of *A. "binotatus"* on Gorgona might refer to *A. medemi.*

Anolis medemi is closely related to *A. maculiventris.* Scale count ranges overlap almost completely. *A. medemi* has 2–3 scales between the supraorbital semicircles, whereas *maculiventris* usually has 3–4, with no (Ecuadorian) or only occasional (Colombian specimens) counts of 2. Other scale counts cannot be distinguished even modally. The color of the male dewlap is nearly identical. Both species almost always have a round dark spot on the back

Table 1. Color and pattern differences between *Anolis medemi* and *Anolis maculiventris*.

Character	*Anolis medemi*	*Anolis maculiventris*
Basic color	rufus, red- or orange brown	brown, olive-brown, brown-gray
Pattern	usually evident, often prominent; dark bars on sides and back of head, body, tail and legs	sometimes prominent, usually none at all; dorsal surfaces seldom barred, if so not prominent
Vertebral region	series of 9–11 more or less prominent spots or bars between head and tail	often dark; usually little or no trace of dark spots or bars between head and tail; sometimes dark spots at top of lateral bars on flanks
Flank region	usually 5–6 darker brown bars, with no tendency to black	bars if present may be nearly black; usually almost completely absent
Back of head	Dark bar over head between eyes present, usually prominent; occipital spot present	little or no pattern; bar between eyes often not prominent; occipital spot usually present

of the head (smaller in *maculiventris*); both may have 5–6 vertical or diagonal bars on the flanks, sometimes separated by series of round yellow spots (much less often seen in *maculiventris*); and both have occasional uniform brown-gray individuals, especially females, with no visible pattern (much more common in *maculiventris*).

The main differences between the two species involve color and pattern (Table 1), adult size and microhabitat. Living and preserved *A. medemi* are basically orange-brown, while *A. maculiventris* is brown, gray-brown or olive-brown, rarely with any orange cast. The darker brown markings are usually much less visible in *A. maculiventris.* Large adult *A. medemi* measure 49–51 mm SVL and weigh (live weight) about 2.0–2.3 g; large adult *A. maculiventris* measure 45–48 mm and weigh 15–17 g. The hemipenes of the two species are illustrated in Figure 4.

Although vegetation and forest structure on Gorgona Island appeared similar to that on the adjacent mainland, most of the

14 specimens collected by our group were found on thin to intermediate diameter tree trunks or larger branches, about 1.5–3.0 m above the ground; one was on the ground. In contrast, *A. maculiventris* is usually seen on twigs, vines or slender branches 0.5–1.5 m above the ground, or on green or dried leaves in open areas near the ground.

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Helen Chin, Fernando Castro, Humberto and Fanny Carvajal, Carlos Galvis H. and Dennis M. Harris provided many of the Colombian *A. maculiventris* specimens. Humberto and Fanny Carvajal collected most of the *A. medemi*. Work in Columbia was sponsored partially by the Universidad del Valle and the Tulane University International Center for Medical Research, grants from the U.S. Public Health Service (NIAID A1-A21511) and the Colombian National Science Foundation COLCIENCIAS (10006-1-07-76), and a COLCIENCIAS grant to Universidad de Los Andes and Henry von Prahl for a multidisciplinary study trip to Gorgona Island in May 1979. Museums listed include: AMNH—American Museum of Natural History, New York; BMNH—British Museum (Natural History), London; CSJ—Colegio San José, Museo de Historia Natural, Medellín; FMNH—Field Museum of Natural History, Chicago; ICN—Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogota; IND-R—INDERENA, Bogota; LACM—Los Angeles County Museum of Natural History, Los Angeles; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge; NHMB—Naturhistorisches Museum, Basel; NHMW—Naturhistorisches Museum, Vienna; SDNHM—San Diego Natural History Museum, San Diego; UMMZ—University of Michigan, Museum of Zoology, Ann Arbor; USNM—United States National Museum, Smithsonian Institution, Washington, DC; UVC—Universidad del Valle, Cali, Departamento de Biologia; ZMB—Zoologisches Museum, Universitaet Humbolt, Berlin.

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LARVAL DEVELOPMENT, RELATIONSHIPS, AND DISTRIBUTION OF *MANDUCUS MADERENSIS*, WITH COMMENTS ON THE TRANSFORMATION OF *M. GREYAE* (PISCES, STOMIIFORMES)

DAVID G. SMITH,[1] KARSTEN E. HARTEL,[1]
AND JAMES E. CRADDOCK[1,2]

ABSTRACT. Larval development of *Manducus maderensis* is described for the first time and additional information is presented on the development of *M. greyae*. Relationships of *Manducus* and its close relative, *Diplophos*, are discussed based on larval pigmentation, transformation size, and the degree of development of annular mucosal intestinal folds. Distribution of *M. maderensis* is updated with extensive new material.

INTRODUCTION

Manducus (Goode and Bean, 1896) occupies a position at or near the base of the teleostean order Stomiiformes; thus it is of considerable interest. Its morphology and relationships have been discussed by Fink and Weitzman (1982) and Ahlstrom *et al.* (1984). Of the two species currently recognized, the larva of only *Manducus greyae* Johnson, 1970 has been described (Ozawa and Oda, 1986). In this paper we describe pretransformation larvae of the second species, *Manducus maderensis* (Johnson, 1890), and provide new information on its distribution. In addition, we describe the transformation of *M. greyae*.

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MATERIALS AND METHODS

The primary material examined by us is from the Woods Hole Oceanographic Institution (WHOI) collections housed at the Museum of Comparative Zoology (MCZ), Harvard University. Additional material from CAS, IOS, ISH, UMML, URI, and USNM was also examined. All institutional acronyms follow Leviton *et al.* (1985).

Counts and measurements follow Hubbs and Lagler (1964), and photophore terminology follows Weitzman (1986:227). Counts of bilateral structures were made on the left side. Specimen size is given as standard length (SL) in mm. Drawings were made with the aid of a Zeiss SV-8 stereo microscope with a camera lucida attachment.

DESCRIPTION OF *MANDUCUS* LARVAE

Manducus maderensis

The larvae of *M. maderensis* can be distinguished from the larvae of other elongate "gonostomatids" by the combination of: (1) pronounced annular mucosal folds along the intestine, (2) a dorsolateral row of chromatophores, and (3) fewer than 40 anal-fin rays.

The smallest specimen, 10.0 mm (MCZ 82191, Fig. 1A), is completely untransformed although notochord flexation is complete. It is moderately elongate with a body depth approximately 9% of SL. The dorsal and anal fins are fully formed. The dorsal fin is located posterior to the midpoint of the body and slightly anterior to the anal-fin origin. The pectoral fin has a well-developed base and blade but lacks rays. The pelvic fins are just beginning to develop and are located slightly less than one dorsal-fin length anterior to the dorsal-fin origin. The preanal length is 70% of SL. The gut consists of a short esophagus, a short sac-like stomach, and a long intestine. The intestine is externally visible and has pronounced annular mucosal folds. A series of 22 dark chromatophores runs longitudinally along the dorsal part of the body, just ventral to the dorsal midline, from the level of the pectoral fin to the end of the caudal peduncle; this series of chromatophores will be referred to as the dorsal series. There is a

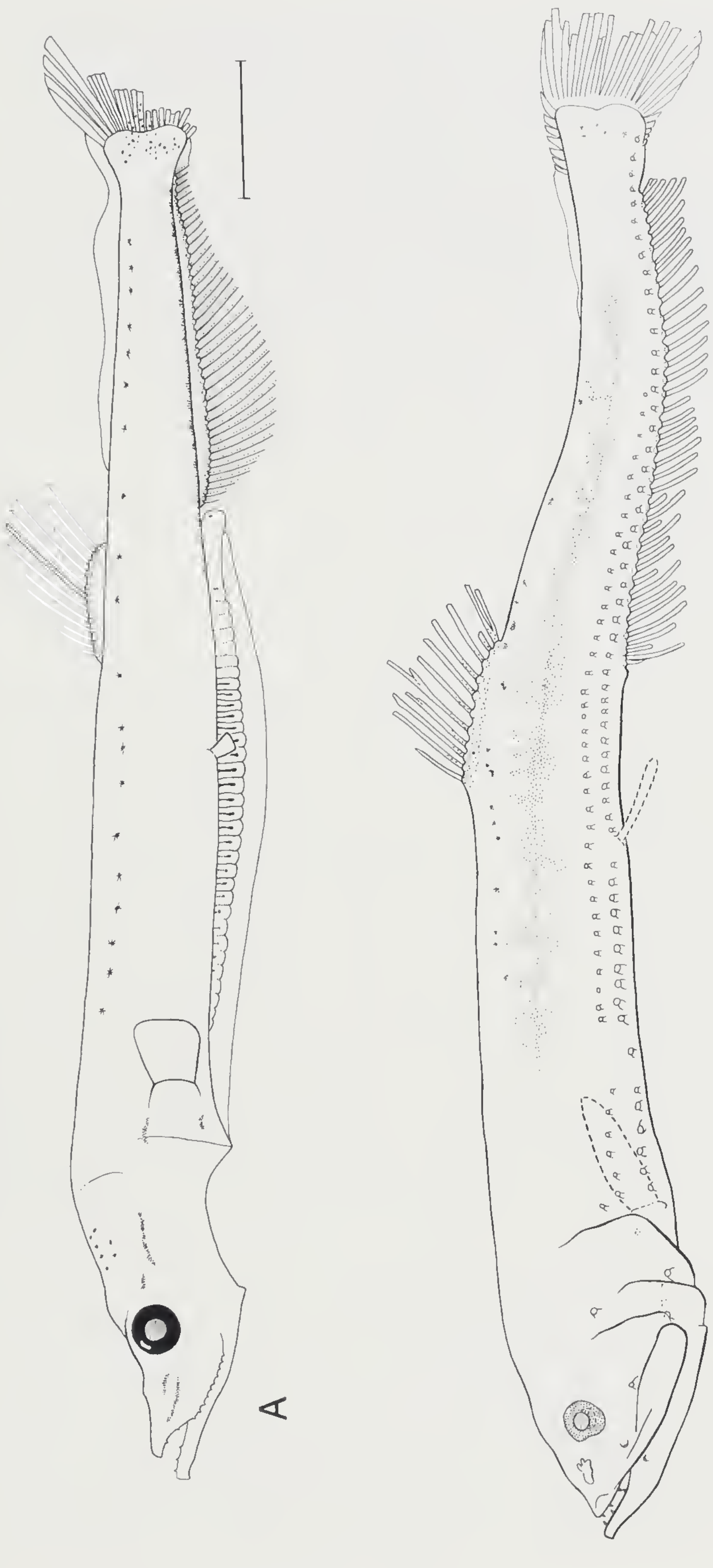

Figure 1. *Manducus maderensis*. A) Larva, 10 mm SL (MCZ 82191). B) Transforming larva, 18 mm SL (MCZ 82194). Drawn by L. Meszoly.

peppering of small melanophores on the dorsal surface of the head posterior to the eyes, and a deep-lying longitudinal streak of pigment on the lateral surface of the head both anterior and posterior to the eye. Additional pigment is found dorsal to the anteriormost part of the esophagus, on the ventral edge of the pectoral-fin base, as a line midventrally on the isthmus, and as a series of minute chromatophores along the ventral edge of the mandible. There is a row of chromatophores along the anal-fin base and a scattering of chromatophores on the base of the tail opposite the hypurals. No photophores are visible, and in alcohol the ground color of the body is completely white (probably semitransparent in life).

The next larger specimen (14.5 mm, MCZ 82190) is damaged. It is untransformed and has no photophores. Pigmentation appears similar to that of the 10-mm specimen.

The third pretransformation specimen is 15.0 mm (MCZ 82189). Like the 10-mm specimen, it shows no trace of photophores or scales and is white. The dorsal series of chromatophores is present from the occiput to the caudal peduncle; the posterior spots in this series are larger than the anterior ones. A row of chromatophores is present internally along the anal-fin base. The remaining pigment is similar to that of the 10-mm specimen.

Transformation occurs somewhere between 15 and 18 mm. Three specimens, 18.0–18.5 mm, are well into the process. An 18.5 mm specimen (MCZ 82192) is still largely white and has no scales. The ventral photophores (the IC and OA series) have formed, but there is no sign of the other lateral photophores. On the head, the BR, SO, ORB, and OP photophores are present (Table 1). Larval chromatophores are still present, including the dorsal series. The adult pigmentation appears to be developing dorsolaterally around the larval chromatophores. The annular mucosal folds of the intestine are still apparent posteriorly. Two specimens, 18.0 and 18.5 mm (MCZ 82194 [Fig. 1B], and 82193), resemble the preceding one, but the adult pigment is more extensive. Larval chromatophores are still present but are partially obscured by the developing adult pigment. Ventral photophores are present, but there is no sign of lateral photophores. A 17.5-mm specimen (MCZ 82174), although slightly smaller than the preceding three, is further along in development. It is uniform light brown in color and the larval chromatophores are no longer visible. Scale pockets are not visible.

Our smallest specimen with lateral photophores is 18 mm (MCZ 82158), and it has only the beginnings of the midlateral series (LLP). The 17-mm specimen figured in Grey (1964; fig. 23) appears slightly more developed. The LLP series lengthens as the fish grows, but the small accessory photophores do not appear until about 30 mm (MCZ 82178). At 24 mm (MCZ 82177) scales are clearly visible. By about 48 mm, *M. maderensis* is fully adult in body form, pigment, and photophore development.

Manducus greyae

Ozawa and Oda (1986:80) described larvae of *M. greyae* based on 15 specimens of 7.5 to 21.4 mm. Their largest specimen was just beginning to transform; hence, they were unable to describe that process fully. The MCZ larval-fish collection contains specimens of *M. greyae* from 22 mm to about 46 mm, a range that encompasses the entire process of transformation. We are thus able to provide an account of transformation in this species.

The earliest stage in transformation is represented by a specimen of 22 mm (MCZ 82462). It is somewhat damaged, but the following photophores appear to be present: SO, ORB, OP, BR, IP, PV, VAV, and AC (Table 2). The OA series is not visible and there are no lateral photophores. The annular mucosal folds of the intestine are clearly visible. The dorsal series of chromatophores is absent, and the only ventral chromatophores visible are located dorsal to the anal-fin base and as a longitudinal midventral streak on the isthmus. Pigment is present just posterior to the tip of the flexed notochord. Some lateral pigment is developing on the myosepta and near the midlateral line, but the fish as a whole is still white.

In six additional specimens ranging from 22 to 24 mm (MCZ 82463 [Fig. 2], 82465, and 82466) the photophore complement is somewhat more complete than in the previous specimen (Table 2). In particular, the IP series increases from two to ten, and the OA series increases from zero to 52. Three of these specimens (23–24 mm) have begun to develop the midlateral photophores (LLP) and three (22–23.5 mm) have not. One of the 24-mm specimens (MCZ 82466) has begun to develop adult pigmenta-

Table 1. Selected counts and measurements for larvae of *Manducus maderensis*.

Specimen	MCZ 82191	MCZ 82190	MCZ 82189	MCZ 82194	MCZ 82192	MCZ 82193
Standard length (mm)	10	14.5	15	18	18.5	18.5
Preanal length (mm)	7	10	10	11	12	11
Dorsal rays	10	—	10	11	10	12
Anal rays	ca. 34	—	ca. 36	36	ca. 35	37
Photophores:						
SO	—	—	—	1	0	1
ORB	—	—	—	2	2	2
OP	—	—	—	3	3	3
BR	—	—	—	9	9	9
IP	—	—	—	12	7	13
PV	—	—	—	17	21	18
VAV	—	—	—	12	13	ca. 11
AC	—	—	—	27	26	29
OA	—	—	—	ca. 44	41	46

Table 2. Selected counts and measurements for transforming larvae of *Manducus greyae*.

Specimen	MCZ 82462	MCZ 82463	MCZ 82463	MCZ 82463	MCZ 82463	MCZ 82465	MCZ 82466
Standard length (mm)	22	22	24	23	23	23.5	24
Preanal length (mm)	12	13	13	13	13	13.5	ca. 14
Greatest depth (mm)	2.5	2.3	2.2	ca. 2.4	ca. 2.2	2.6	ca. 2.0
Photophores:							
SO	1	1	1	1	1	1	1
ORB	d	3	3	3	3	3	3
OP	3	3	3	3	3	3	3
BR	11	11	13	12	13	11	12
IP	2	7	7	9	10	9	d
PV	18	20	20	20	21	21	d
VAV	10	13	14	13	15	14	12
AC	24	35	36	40	35	36	40
OA	0	ca. 30	ca. 48	51	52	42	d
LLP	–	–	+	–	+	–	+
Acc. LP	–	–	–	–	–	–	–
Intestine	exposed	exposed	exposed	exposed	exposed	exposed	exposed
Adult pigment	–	–	–	–	–	–	+

Key to symbols: d (specimen damaged, character obscured); – (character absent); + (character present).

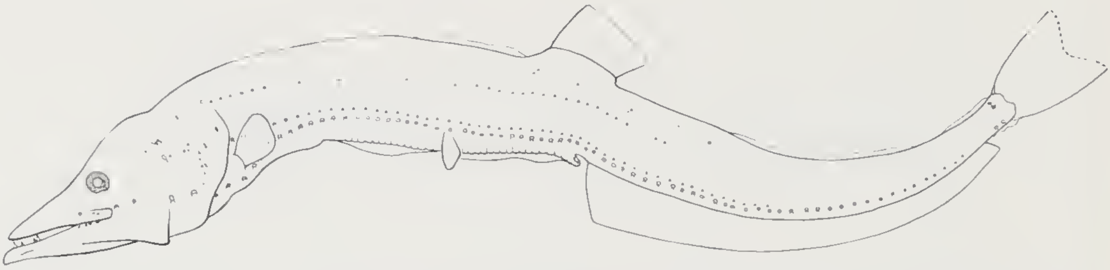

Figure 2. Transforming larva of *Manducus greyae*, 24 mm SL (MCZ 82463). Drawn by L. Meszoly.

tion, the esophagus and stomach are black, and it is the only one of these specimens in which the intestine has withdrawn inside the contours of the body. The second 24-mm specimen (MCZ 82463) is still white. The smallest specimen that shows the accessory lateral photophores is 30 mm (MCZ 82464). By 46 mm the species is largely adult in body form, pigmentation, and photophore development.

Ozawa and Oda (1986:82) claimed that in *M. greyae* the midlateral photophores develop before the ventral photophores. This is not the case in the specimens examined by us. The ventral photophores, especially the IC series, are well developed and conspicuous before the LLP series begins to appear. In this, *M. greyae* resembles all the other species in *Manducus* and *Diplophos* that we have examined.

Manducus–Diplophos Relationships

Opinions and evidence about the status of *Diplophos* Günther, 1873 and *Manducus* Goode and Bean, 1896 have differed among authors and over the years. Goode and Bean (1896:514) established *Manducus* to contain *Gonostoma maderense* Johnson, 1890. While they recognized that this species was not a true *Gonostoma,* they did not comment on any resemblance to *Diplophos taenia* Günther. Grey (1960:76) reduced *Manducus* to a subgenus of *Diplophos* because the distinction between the two nominal genera (i.e., differences in certain proportional measurements and numbers of fin rays, photophores, and vertebrae) seemed trivial compared to differences among other gonostomatid genera. Johnson (1970:442) went further and concluded that even subgeneric rank was unwarranted. His new species, *Diplophos greyae,* seemed to him to be intermediate between the type species of the two nominal genera. Mukhacheva (1978) reviewed *Diplophos* on a worldwide basis, recognizing four species (*taenia, rebainsi* Krefft and Parin, 1972, *greyae,* and *maderensis*) and agreed with Johnson (1970) that subgenera are unnecessary. Fink and Weitzman (1982) described the osteology of *taenia* and *maderensis* and treated them both as *Diplophos.* Ahlstrom *et al.* (1984), however, resurrected *Manducus* based on the condition of the pectoral-fin radials. *Manducus* has the cartilages of the third and fourth proximal radials separate, and the ninth distal radial is in line with the others; *Diplophos* has the cartilages (though not the bones) of the third and fourth proximal radials fused, and the ninth distal radial is out of line with the others (see figs. 18 and 19 in Fink and Weitzman, 1982). These authors recognized two species in each genus: *Diplophos taenia, D. rebainsi, Manducus maderensis,* and *M. greyae.* Ozawa and Oda (1986) recognized seven species, all in *Diplophos.* Ozawa *et al.* (1990) revised the *D. taenia* complex, which includes four species: *D. taenia, D. proximus* Parr, *D. orientalis* Matsubara, and *D. australis* Ozawa *et al.*

The species of *Diplophos* and *Manducus* represent the most primitive of the stomiiform fishes (Fink and Weitzman, 1982; Ahlstrom *et al.*, 1984; Fink, 1984). *Diplophos* shares one derived feature, the partially fused third and fourth proximal radials, with the Photichthyidae (an ill-defined group) and Stomiidae, but *Manducus* retains the primitive state of this character. Ahlstrom *et al.* (1984:198) were unable to find any derived characters that would unite *Diplophos* and *Manducus* as a stomiiform subgroup. Early-life-history characters could not be used because the larvae of *M. maderensis* and *M. greyae* were unknown at the time.

Larvae of *D. taenia* are distinguished by their elongate body and the conspicuous series of dorsal and ventral chromatophores (Ahlstrom *et al.*, 1984: fig. 98; Ozawa and Oda, 1986: fig. 2). The intestine has pronounced annular mucosal folds. The dorsal fin is located slightly anterior to the anal fin. Larvae of *D. orientalis* closely resemble those of *D. taenia* but are somewhat less elongate and transform at a smaller size (ca. 30 mm vs. 50 mm; Ozawa and Oda, 1986:77, fig. 3). Larvae of *M. greyae* resemble those of *D. taenia* and *D. orientalis* but are shorter-bodied and have less conspicuous dorsal and ventral chromatophores (Ozawa and Oda, 1986:81, fig. 5); in larger larvae, the dorsal series disappears. The intestine has pronounced annular mucosal folds as in *D. taenia, D. orientalis,* and *M. maderensis. Manducus greyae* transforms at about 21–24 mm. Larvae of *M. maderensis* resemble those of *M. greyae* in their short body and inconspicuous dorsal and ventral chromatophores (Figs. 1A–B). The dorsal chromatophores are better developed than those of *greyae* and remain throughout the larval stage, but the ventral chromatophores are present only over the anal-fin base. *Manducus maderensis* transforms at a smaller size (15–18 mm) than any of the other species.

The larvae of the species of *Diplophos* and *Manducus,* then, differ primarily in their relative body depth, the extent of dorsal and ventral pigmentation, and the size at metamorphosis. Even these characters show a certain amount of gradation among the species. *Diplophos orientalis* is intermediate between *D. taenia* and *M. greyae* in both body depth and size at metamorphosis. *Manducus maderensis* has a relatively deep body, like *M. greyae,* but its dorsal pigmentation is stronger and more persistent through growth. The most striking similarity between the larvae of all these species is the pronounced annular mucosal folds of the intestine.

In assessing the significance of these larval characters, we face the same problem as in assessing the significance of adult characters: to find shared specializations that link *Manducus* and *Diplophos* to each other or to other stomiiform genera. Ahlstrom *et al.* (1984) were able to find only one adult synapomorphy that links *Diplophos* to photichthyids and stomiids (the condition of the pectoral-fin radials) and no synapomorphies that link *Manducus* to any other stomiiform genus. The larval characters described in the present paper do not alter this situation. The resemblances between larvae of the species of *Diplophos* and *Manducus* are considerable, but none of these characters is clearly specialized below the ordinal level. Similarities in body shape and pigmentation could simply represent the primitive stomiiform condition. Even the most conspicuous character shared by larvae of *Diplophos* and *Manducus,* the annular mucosal folds of the intestine, is a matter of degree of expression rather than presence or absence. Other stomiiformes have mucosal folds although they are not as pronounced. Indeed, a similar intestine is found in a

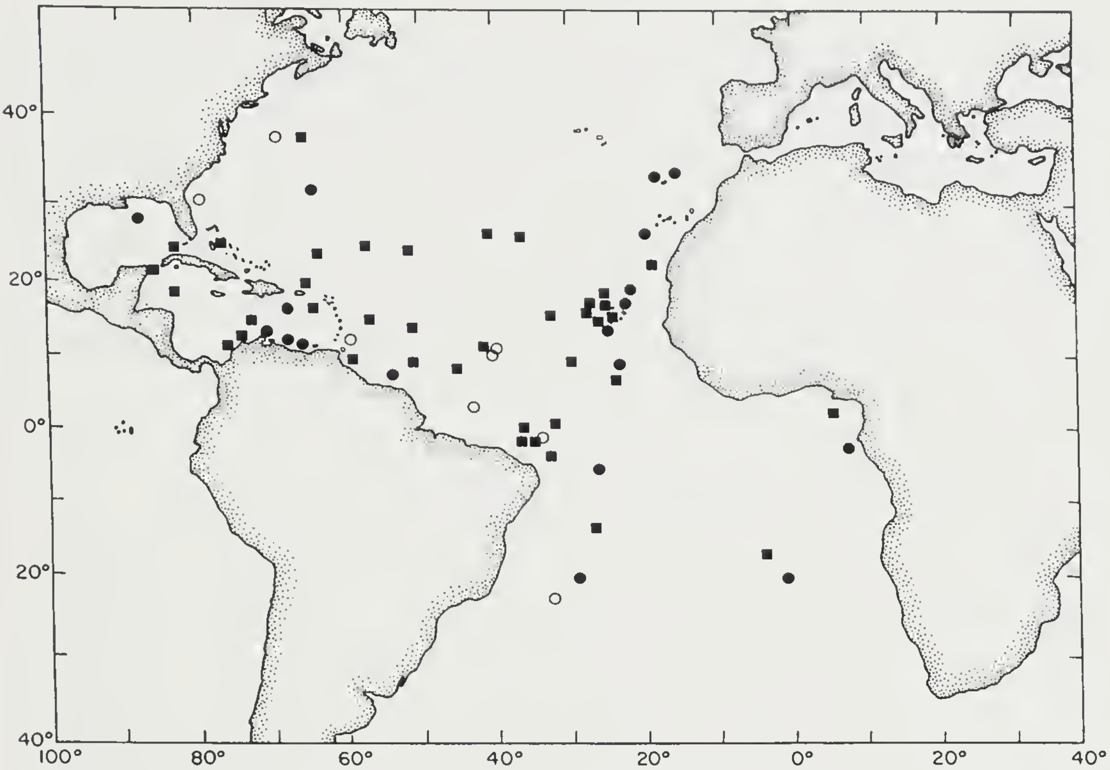

Figure 3. Distribution of *Manducus maderensis* based on all known material; ○ = specimens <18.5 mm, ■ = >19 mm, and ● = >95 mm. Symbols may represent more than one specimen or collection.

variety of lower teleosts, including clupeids, engraulidids, and certain myctophids. Whether these mucosal folds are identical structurally and developmentally in all the taxa that possess them is unknown. A phylogenetic analysis of larval characters in stomiiform fishes is clearly beyond the scope of the present paper, and without such analysis the significance of these characters cannot be determined. Clearly much work remains to be done before a useful phylogeny of stomiiformes can be constructed. In the meantime, we offer the present study as one more piece of a puzzle that may one day be assembled into a coherent picture.

DISTRIBUTION

At the time of Grey's (1960 and 1964) revisions of the "Gonostomatidae" *M. maderensis* was known from fewer than 50 specimens. Of these, 31 were adults, all from near land—at Madeira in the eastern Atlantic, and off Suriname and Mississippi in the western Atlantic. The 16 juveniles (<90 mm) were from the central North Atlantic (11 specimens), near the Bahamas (4), and the

South Atlantic off Brazil (a single specimen from 0°22′S). Based on these records and five additional specimens (two of them from between 1° and 2°S off Brazil), Mukhacheva (1978) published a map of the distribution of *M. maderensis* and considered the species to be distant neritic, being "endemic to the western and eastern parts of the central Atlantic . . . but . . . absent in the open waters." She was correct in that it is probably land-associated, especially when adult, but, according to more recently collected data, it also occurs in the open ocean both when young and as an adult (Fig. 3). *Manducus maderensis* is endemic to the Atlantic Ocean, occurring primarily in the tropics and the equatorward halves of the subtropical gyres (tropical-semisubtropical pattern of Backus *et al.*, 1977); it is now known from 37°39′N to 23°02′S.

There are only 13 specimens known from the South Atlantic, none of them from the poleward half of the subtropical gyre. Its rarity there is probably a reflection of the low fishing effort. In the North Atlantic, however, there are many specimens from the poleward half of the subtropics; most of these are adults from near Madeira (Maul, 1948; Grey, 1964; ISH, IOS). In the northern Sargasso Sea, there are but five specimens—three Gulf Stream waifs (MCZ 82193, 82194, and 88254) and two specimens reported by Bond (1974) from Ocean Acre off Bermuda (USNM 248766 and MCZ 91350, ex URI).

Since few specimens of *M. maderensis* have been collected with opening/closing nets, we can say little with precision about its vertical distribution, especially at the deeper limit of its depth range. We can say, however, that it occurs in the upper mesopelagic zone (about 450–600 m) at the edge of continental (and island) slopes and in the open ocean. The species makes a diel vertical migration into the upper 100 m at night at sizes between 20 and 100 mm. The shallowest records of large adults are the 177 mm individual at 200 m (ISH 748/66) and the 209 mm gravid female (MCZ 91350) from off Bermuda at 150 m. Of the 193 known specimens, 55, between 18 and 64 mm, were collected with neuston nets at the very sea surface.

LIST OF MATERIAL

The following *M. maderensis* (141 specimens, 10 to 220 mm) have been collected since the papers of Grey (1964) and Mukhacheva (1978), or were not reported by them. Each entry contains the museum catalog number, the number and size(s) of specimens, and collection data (station number, position, maximum depth reached by net, and the time of the beginning of the collection). Specimens not examined by us are marked with an asterisk. The collections at ANSP, GCRL, GMBL, MZUSP, ZMUC, TCWC, USF, SAM, and VIMS have no *M. maderensis*. Also included is the material of *M. greyae* used for the transformation description.

Manducus maderensis

IOS Discovery

7089#03* (2:31–42) 17°41′N, 25°23′W, surface, 0145 hrs.; 7089#12* (3:19–24) 17°34′N, 25°26′W, surface, 0245 hrs.; 7089#13* (2:18–21) 17°48′N, 25°29′W, 515–600 m, 0950 hrs.; 7089#21* (9:21–26) 17°52′N, 25°27′W, surface, 2145 hrs.; 7089#26* (5:22–41) 17°52′N, 25°25′W, surface, 2100 hrs.; 7089#27* (2:@ 22) 17°52′N, 25°25′W, 25–60 m, 0138 hrs.; 7089#32* (6:20–25) 17°45′N, 25°22′W, surface, 0100 hrs.; 7089#37* (1:28) 17°50′N, 25°29′W, surface, 0145 hrs.; uncat.* (1:220) off Madeira.

ISH

64/66* (1:163) WH 177/66, 33°45′N, 16°00′W, 600 m, 2110 hrs.; 296/66* (3:145–167) WH 181/66, 19°11′N, 21°58′W, 460 m, 2100 hrs.; 399/66* (8:52–82) WH 183/66, 6°30′N, 24°33′W, 50 m, 2100 hrs.; 620/66* (1:163) WH 187/66, 5°34′S, 26°58′W, 320 m, 2000 hrs.; 748/66* (1:173) WH 191/66, 21°00′S, 30°00′W, 200 m, 2000 hrs.; 313/68* (1:177) WH 8-III/68, 26°10′N, 19°26′W, 580 m, 2233 hrs.; 1125/68* (1:56) WH 20-III/68, 13°56′S, 27°38′W, 580 m, 2255 hrs.; 1665/71* (1:157) WH 443/71, 21°35′S, 2°00′W, 2,100 m, 2025 hrs.; 2742/71* (1:98) WH 498-I/71, 17°22′N, 22°58′W, 105 m, 1955 hrs.; 2819/71* (1:125) WH 498-III/71, 17°27′N, 22°55′W, 610 m, 2203 hrs.

MCZ

52541 (5:48–52) SUN1207, 9°16′N, 27°55′W, surface, 0015 hrs.; 52566 (1:44) RHB1290, 21°17′N, 85°22′W, 124 m, 0020 hrs.; 54303 (1:110) Oregon 2007, 7°34′N, 54°49′W, 445 m; 56952 (1:145) RHB3052, 11°22′N, 65°01′W, 350 m, 1700 hrs.; 61476 (1:96) RHB2290, 2°57′S, 8°05′E, 75 m, 2005 hrs.; 82170 (1:70) RHB2269, 18°33′S, 4°00′W, 100 m, 2005 hrs.; 82171 (1:49) RHB1207, 9°16′N, 27°55′W, 51 m, 0010 hrs.; 82172 (1:61) RHB 1266, 12°44′N, 74°10′W, 575 m, 1255 hrs.; 82173 (1:130) Oregon 4419, 11°43′N, 69°13′W, 455 m; 82174 (1:17.5) RHB966, 1°13′S, 34°35′W, 102 m, 0335 hrs.; 82175 (1:48) RHB1253, 16°38′N, 64°27′W, 133 m, 0038 hrs.; 82176 (1:29) RHB1286, 19°46′N, 83°07′W, 86 m, 0010 hrs.; 82177 (1:24) RHB2035, 22°25′N, 19°00′W, 500 m, 0845 hrs.; 82178 (1:30) RHB2069, 15°23′N, 24°28′W, 320 m, 0420 hrs.; 82179 (1:22) RHB2077, 15°30′N, 26°12′W, 95 m, 2135 hrs.; 82180 (2:33 & 41) RHB2084, 17°12′N, 27°59′W, 80 m, 0215 hrs.; 82181 (1:20) RHB2095, 25°52′N, 36°48′W, 140 m, 2110 hrs.; 82182 (1:19) RHB2930, 11°00′N, 41°31′W, 475 m, 0055 hrs.; 82183 (1:61) RHB2946, 9°03′N, 51°05′W, 510 m, 0220 hrs.; 82184 (1:73) RHB2979, 13°34′N, 50°50′W, 490 m, 0210 hrs.; 82185 (1:20) SUN2078, 15°43′N, 26°28′W, surface, 0120 hrs.; 82186 (2:22 & 52) SUN2083, 17°08′N, 27°55′W, surface, 0001 hrs.; 82187 (2:25 & 27) SUN2101, 26°37′N, 41°18′W, surface, 0005 hrs.; 82188 (1:49) SUN1313, 23°55′N, 83°12′W, surface, 0034 hrs.; 82189 (1:15) RHB2924, 10°59′N, 40°22′W, 490 m, 2330 hrs.; 82190 (1:14.5) RHB2923, 11°00′N, 40°10′W, 500 m, 2045 hrs.; 82191 (1:10) RHB2966, 12°21′N, 59°34′W, 495 m, 0035 hrs.; 82192 (1:18.5) MOC10-137,4, 30°08′N, 79°30′W, 140–160 m, 0254 hrs.; 82193 (1:18.5) SUN9452, 37°36′N, 69°03′W, surface, 0115 hrs.; 82194 (1:18) same data as 82193; 82197 (2:79 & 84) RHB982, 6°51′S, 33°34′W, 85 m, 2105 hrs.; 82198 (1:40) SUN2958, 9°13′N, 59°06′W, surface, 0115 hrs.; 82199 (1:57) RHB1222, 13°55′N, 57°00′W, 300 m, 2300 hrs.; 82200 (1:64) same data as 82198; 88250 (1:18) SUN1431, 23°02′S, 32°15′W, surface, 0120 hrs.; 88251 (1:29) SUN3102, 22°57′N, 64°12′W, surface, 2020 hrs.; 88252 (1:19) SUN2966, 12°21′N, 59°34′W, surface, 0035 hrs.; 88253 (1:62) JEC7741, 8°33′N, 44°37′W, 100 m, 0155 hrs.; 88254 (1:48) KEH7716, 37°00′N, 65°38′W, surface, 0325 hrs.; 88255 (1:29) SUN1253, 16°38′N, 64°27′W, surface, 0030 hrs.; 88256 (1:27) JEC7745, 9°15′N, 46°50′W, 100 m, 0300 hrs.; 88257 (1:24) JEC7712, 0°01′N, 37°40′W, 80 m, 2235 hrs.; 88258 (1:18)

JEC7705, 3°08′N, 42°52′W, 25 m, 0130 hrs.; 91350 (1:220) Ocean Acre 12-55N, 32°11′N, 64°10′W, 150 m, 2240 hrs.

UMML

14824 (1:32) Gerda 205, 23°20′N, 82°55′W, 1,000 m, 1843 hrs.; 22740 (1:156) Pillsbury 455, 13°01′N, 71°55′W, 1,445 m; 23074 (1:29) P-383, 10°19′N, 75°59′W, 70 m, 0101 hrs.; 27541 (2:53 & 58) P-384, 10°24′N, 75°58′W, 40 m, 0302 hrs.; 27747 (6:17–45) P-302, 2°26′N, 4°51′E, surface, 0230 hrs.; 29036 (1:22) P-821, 19°07′N, 65°28′W, 3,000 m, 1145 hrs.

CAS

61060 (1:124) Oregon II 46092, 18°27′N, 67°15′W, 1,499 m, 0852 hrs.

USNM

186282 (5:85–128) Oregon 2007, 7°34′N, 54°49′W, 445 m; 186364 (14:90–140) Oregon 2008, 7°38′N, 54°43′W, 490 m; 248711 (1:27) Ocean Acre 1-18C, 32°10′N, 63°48′W, 100 m, 0145 hrs.

Manducus greyae

MCZ

75518 (1:43) GRH1046, 12°38′S, 148°55′E, 3,240 mwo, 1740 hrs.; 82462 (1:22) GRH1011, 6°25′S, 152°09′E, 2,380 mwo, 0000 hrs.; 82463 (4:22–24) GRH1014, 4°55′S, 152°30′E, 2,380 mwo, 0015 hrs.; 82464 (2:29 & 30) GRH1017, 6°54′S, 152°06′E, 2,380 mwo, 2245 hrs.; 82465 (2:24 & 47) GRH1016, 6°43′S, 152°14′E, 2,380 mwo, 1840 hrs.; 82466 (1:24) GRH1069, 7°44′S, 151°05′E, ca. 1,950 m, 0001 hrs.

Comparative material

Larvae and transforming specimens of the following taxa in the MCZ larval fish collection were examined (number of specimens examined is given in parentheses): *Bonapartia pedaliota* (215), *Cyclothone* spp. (1,092), *Diplophos taenia* (36), *Gonostoma atlanticum* (1,157), *G. denudatum* (282), *G. elongatum* (547), *Ichthyococcus* (97), *Margrethia obtusirostra* (54), Maurolicine cf. “alpha" (4), *Maurolicus muelleri* (269), *Photichthys argenteus* (1), *Pollichthys mauli* (79), *Valenciennellus tripunctulatus* (553), *Vinciguerria attenuata* (1,059), *V. nimbaria* (1,807), *V. poweriae* (825), *Yarella blackfordi* (1).

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A PERUVIAN PHENACOSAUR (SQUAMATA: IGUANIA)

Ernest E. Williams[1] and Russell A. Mittermeier[2]

Abstract. A small lizard from Venceremos, Department of San Martin, Peru, is identified as a hatchling *Phenacosaurus* and possibly the third known specimen of *Phenacosaurus orcesi* Lazell, 1969. It is the first known specimen of the genus from Peru.

INTRODUCTION

The anoline lizard genus *Phenacosaurus* was initially known only from Colombia. Its type species, *P. heterodermus,* was described by A. Duméril, 1851, in Duméril and Duméril (1851), from numerous specimens from "Nouvelle Grenade," the name of Colombia at that time (including Panama). Dunn (1944) added two more Colombian species, *P. nicefori* ("vicinity of Pamplona, Norte de Santander") and *P. richteri* ("Tabio, Cundinamarca"), and Hellmich (1949) still another, *P. paramoensis* ("Paramo de Sumapaz" at the border between Cundinamarca and Meta). The latter two have since been synonymized with *P. heterodermus* (Lazell, 1969). A new giant Colombian species has very recently been described (*P. inderenae* Rueda and Hernandez-Camacho, 1988, from Gutierrez, Department of Cundinamarca).

Specimens or species known or suspected to be from adjacent

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countries have, however, been reported. A specimen from the Sierra de Perija (Museo de Historia Natural La Salle, Caracas 4477), regarded by both Aleman (1953) and Lazell (1969) as *P. nicefori,* is from a peak (Cerro Tetari) in Zulia, Venezuela. (It is probably an undescribed species.) The Field Museum's *P. nicefori* (FMNH 5684) from "Páramo de Taná," cited by Lazell (1969), may, as Rueda and Hernandez-Camacho (1988) have commented, be from Venezuela and not Colombia, since the locality given is precisely at the border between the two countries. The latter problem is rendered moot by more recent collections, since *P. nicefori* is now known from unpublished material from Betania, State of Táchira, further inside Venezuela (specimens in the collections of the Museo de Ciencias Naturales, Caracas, and the Museum of Natural History, Kansas), and a small series of an undescribed phenacosaur has been collected by the expeditions to the Cerro de La Neblina, State of Amazonas, in the extreme south of Venezuela. (These are under study by Charles Myers.) Still another phenacosaur, a single specimen in the collection of the Museo de Ciencias Naturales La Salle, Caracas, has been collected by S. Gorzula and A. Farrera on the Massif de Chimantá, a tepuy in the State of Bolivar, in southeastern Venezuela (to be described by Williams, Prasiderio, and Gorzula).

From Ecuador, Lazell, in his 1969 revision, has described the very distinctive species *P. orcesi* on the basis of two specimens, the type from "Mt. Sumaco," Napo Province, and a paratype from "between L'Alegria [*sic*] and La Bonita," both localities in the Sucumbios Province (formerly the northwest part of the Napo Province). Only recently, specimens of another giant species of phenacosaur have been collected at La Alegria and adjacent localities (specimens in the Museo Ecuatoriano de Ciencias Naturales, the Escuela Politecnica Nacional, the National Museum of Natural History, and in the Museum of Comparative Zoology, to be reported on by EEW and collaborators).

Now a juvenile phenacosaur (MCZ 165211) has been collected in Peru at Venceremos, in the northern part of the Department of San Martin, very near the Department of Amazonas border. This juvenile, both because it is small and immature and because it is not ideally preserved, is conservatively regarded as the third known specimen of *Phenacosaurus orcesi* despite the great dis-

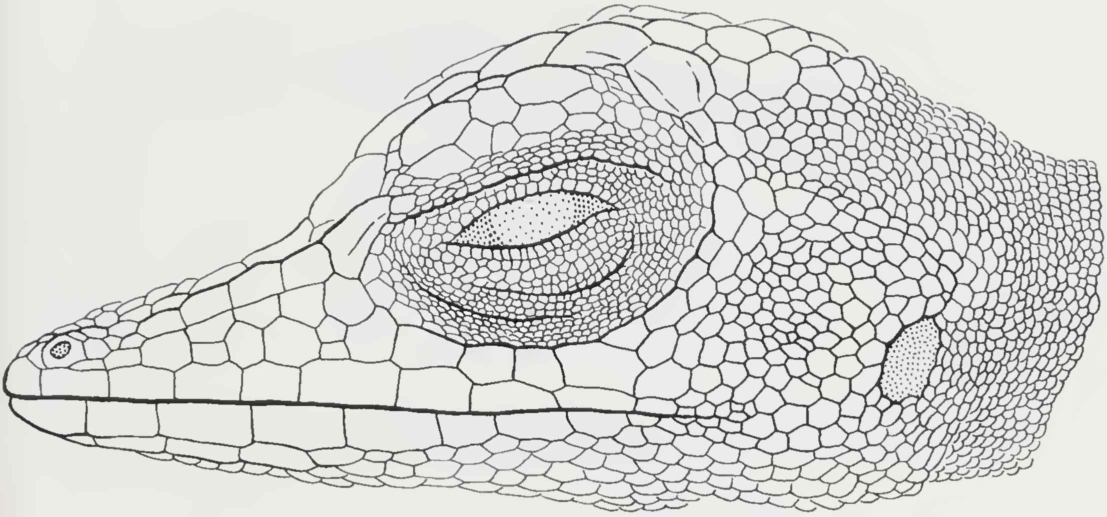

Figure 1. *Phenacosaurus orcesi* juv., MCZ 165211. Lateral view of head. (Right side reversed.)

tance between it and the nearest other specimen of that species, the type from Mt. Sumaco. The new specimen is important enough to deserve detailed description, provided below in a format elaborated from the one that has been used by the senior author in descriptions of *Anolis* over many years (see also Figs. 1–4).

DESCRIPTION

Head

No trace of a casque, not even the ridges that bound the parietal region in adults of the smaller species. All scales smooth.

Dorsal Head Scales. Antorbital region: Rostral much wider than long. Four postrostrals, these defined as all those scales posteriorly in contact with the rostral and therefore including the left circumnasal that has a narrow contact on that side. The right circumnasal is excluded from the rostral by a postrostral. Circumnasals round or ovoid, the nostril nearly central. No differentiated anterior or inferior nasals. Each circumnasal broadly in contact with the first supralabial of its side. Three scales between the circumnasals dorsally. Scales posterior to the circumnasals much smaller than the anteriormost canthals, the scales of the frontal area, or the median series of three scales anterior to the frontal area.

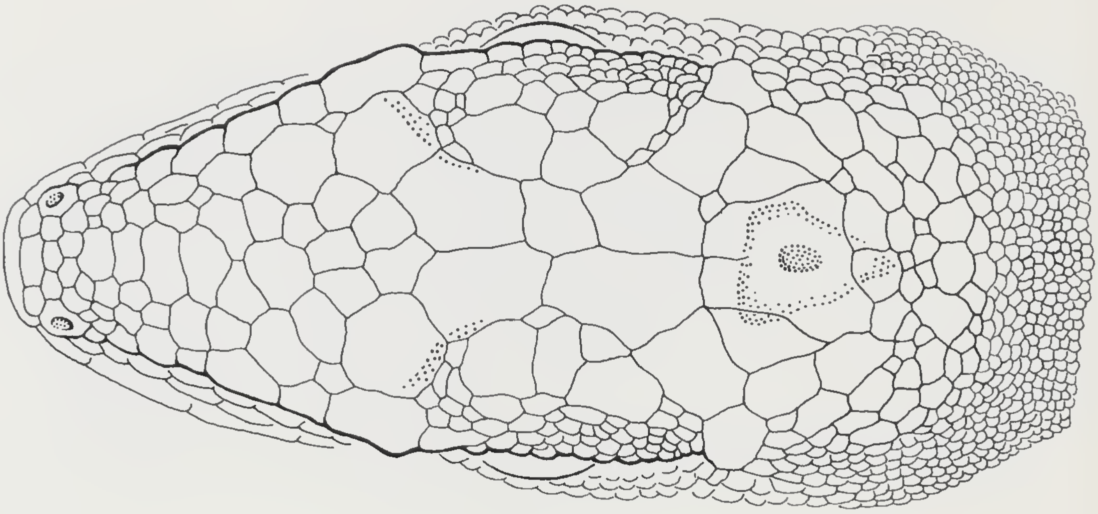

Figure 2. *P. orcesi* juv., MCZ 165211. Dorsal view of head.

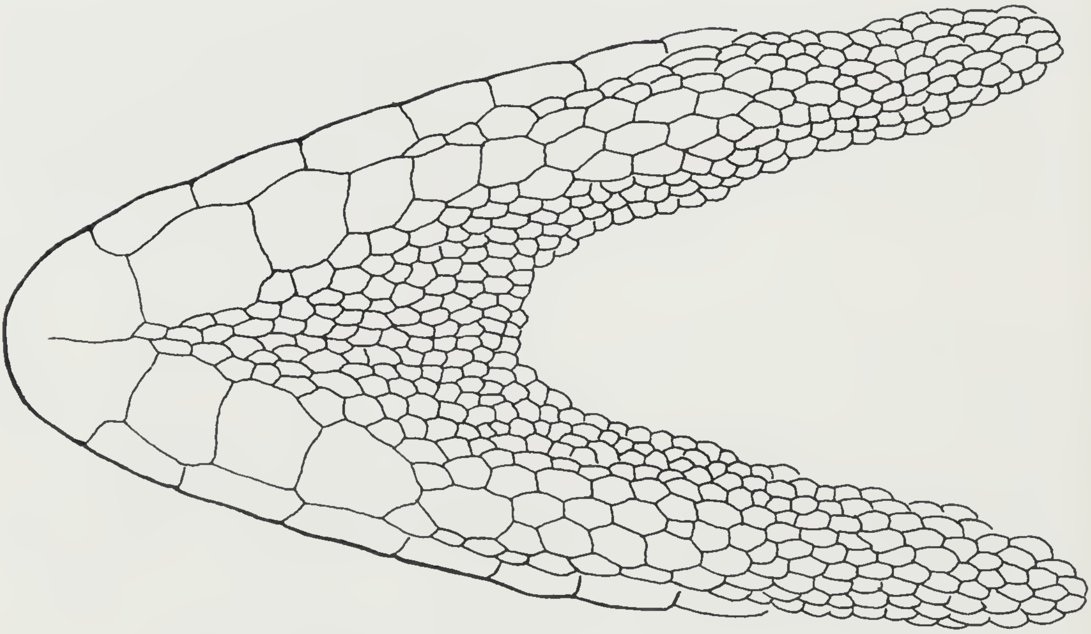

Figure 3. *P. orcesi* juv., MCZ 165211. Ventral view of head.

Frontal depression very shallow. Scales of the frontal area moderately large, polygonal, markedly varying in size. No rosette of larger scales surrounding smaller central scales. Four to six scales between the anterior canthals depending upon where the count is made.

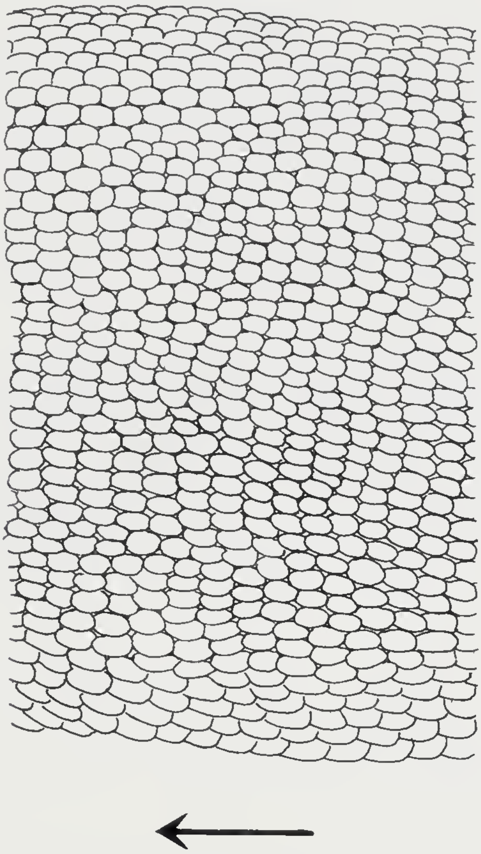

Figure 4. *P. orcesi* juv., MCZ 165211. Lateral view of body scales. Arrow points anteriorly.

Canthals five on each side, gently arched, not keeled, the first (= the posteriormost) largest on both sides, those on the right side grading smaller anteriorly, on the left side the third and fifth larger.

Orbital region: Scales of the supraorbital semicircles large, two scales on the left side in broad contact with three on the right. The two largest supraocular scales in contact with the semicircles on each side. The next largest supraocular on the right side separated from the semicircle of its side by granules; the comparable scale on the left in contact with a lateral supraocular scale. The other scales of the supraocular areas variable in size, smaller laterally. Two to four rows separate the largest supraocular scales from the superciliaries. On each side the two anteriormost superciliaries larger and elongate, the remainder subgranular.

Parietal region: A parietal eye indicated by a light spot. The interparietal apparently fused with other scales: as indicated by an anterior median partial sulcus, by the marked asymmetry of this, the largest scale in the parietal region, and by the slight depression containing the parietal eye, which does not at all correspond to the scale boundaries. The scales lateral to the interparietal strikingly larger than those posterior to it, although these again are sharply distinct from the nape scales. About five rows in the approximate midline between the interparietal and the nape scales. A penultimate row of the posterior parietal scales markedly enlarged.

Lateral Head Scales. Loreal rows three on the right side, two on the left. Total loreals on the right side 11, on the left 10. Two preoculars (defined as the scales below the anterior corner of the eye) on each side, the uppermost in contact with the sulcus between the first and second canthals. Four suboculars on the right side, three on the left. Postoculars ill-defined, grading into the lower temporals.

Temporals in two areas, upper and lower, separated by the double row of slightly enlarged scales on the low ridge that indicates the lower border of the skeletal supratemporal fenestra.

Lower temporals smallest centrally; the upper temporals more nearly subequal but slightly larger anteriorly.

Ear many times the size of any adjacent scale, but much smaller than the (probably compound) interparietal.

Supralabials more or less elongate rectangles, seven to nine below the center of the eye.

Ventral Head Scales. Mental very deep, as deep as wide, almost wholly divided by a median sulcus, slightly indented by two very small medial gulars between the very large first sublabials. Three sublabials on each side in contact with the infralabials. Six to eight infralabials to below the center of the eye.

The anterior gulars (those posterior to the medial gulars that are in contact with the mental) small, elongate, slightly swollen, larger than the central gulars posterior to them, but not as wide. The latter becoming more granular and more imbricate near the median insertion of the dewlap but larger and still juxtaposed next to the sublabial series of each side. Lateral gulars intervening between the sublabials and the infralabials at the level of the third sublabials, after which it becomes impossible to distinguish between lateral gulars, sublabials, and the lateralmost central gulars. All gulars subgranular posteriorly alongside the dewlap.

Trunk

No trace of a middorsal crest. Dorsal and flank scales subequal, smooth or subimbricate, or (flank scales) sometimes with tiny granules visible between them. Ventrals larger, smooth, slightly convex, very weakly imbricate, in transverse rows.

Limbs

Scales smooth, anteriorly larger and imbricate on lower arm and lower leg, separated by naked skin on upper arm and thigh, posteriorly granular on upper arm and thigh but not so on lower arm and leg. Supradigitals smooth or very weakly carinate, widened transversely, lamella-like. Lamellae under phalanges ii and iii of fourth toe ca. 21.

Tail

Curving at tip as though prehensile, weakly compressed, all scales weakly keeled, without a dorsal crest, but the middorsal row imbricate and weakly dentate. Enlarged postanals (male) small but distinctly larger than surrounding scales.

Dewlap

Strongly indicated (juvenile male), distinguished by the longitudinal orientation of its scales and extending onto belly beyond the insertion of the arms. Edge scales smaller than ventrals, lateral scales larger than edge scales but, perhaps, smaller than ventrals.

Size

Snout–vent length 32 mm; tail length 43 mm.

Color in life

(from kodachromes by Russell Mittermeier)

Ground color cream mottled with brown. Dark brown streaks radiating from eye onto supralabials and toward ear. Dorsum with three broad dark brown bands variegated with lighter brown. Interstices of bands more or less vermiculate with darker brown. Limbs banded brown and cream. Small dewlap pinkish or orangish with sparse black spotting.

Locality

Collected 14 December 1983 by Russell Mittermeier near Venceremos ("few houses along the road"): "km 390–391 on the road between Rioja (6°05′S, 77°09′W) and Pedro Ruiz Gallo (= Ingenio, ca. 5°56′S, 77°59′W), approximately 91–92 km from Rioja; downhill into the forest about one km from the road, on the forest floor, within ca. 100 m of a small rainforest stream; elevation 4,750 ft in steep montane terrain, forest floor well covered with moss and humus." The locality is cloud forest with moss-covered trees and a springy, mossy floor. Much of the World Wildlife Fund film *Monkey of the Clouds* was shot in the area. The juvenile phenacosaur was the only herpetological specimen taken at Venceremos in 1983. In 1978, frogs were collected: a number of frogs not yet identified, a species of *Eleutherodactylus,* two undescribed species of *Colostethus,* and toads of the *Bufo granulosus* and *B. typhonius* complexes.

Discussion

Because this specimen is a juvenile it lacks the casque that is one of the defining characters of adult phenacosaurs, but a casque is absent in all juvenile *Phenacosaurus* (MCZ 14165: *P. heterodermus,* 30 mm SVL; EPN 2218: *P. sp.* 38 mm SVL). It also lacks the differentiated large round flat flank scales separated by granules, characteristic of *P. heterodermus,* the type species of the genus, and present also in *P. nicefori* and *P. inderenae* (but these are quite absent in the third described species, *P. orcesi*). In this juvenile there is no trace of the median crest present in most phenacosaurs (but absence as an individual variation has been demonstrated [in adults] for *P. heterodermus* [Lazell, 1969] and occurs also in the adult paratype of *P. orcesi*). The Peruvian juvenile has two loreal rows on each side and only nine loreal scales on one side, 10 on the other, the *unmodified* circumnasal scale broadly in contact with the first supralabial, and a short tail, very little longer than snout–vent length, with a curvature suggestive of prehensility. All are characters congruent with determination as a member of the genus *Phenacosaurus.* It is clearly closest to the two known adult specimens of *P. orcesi,* which it matches in the absence of enlarged flat round flank scales. Figures 5–7 display the head of the paratype of that species, which has

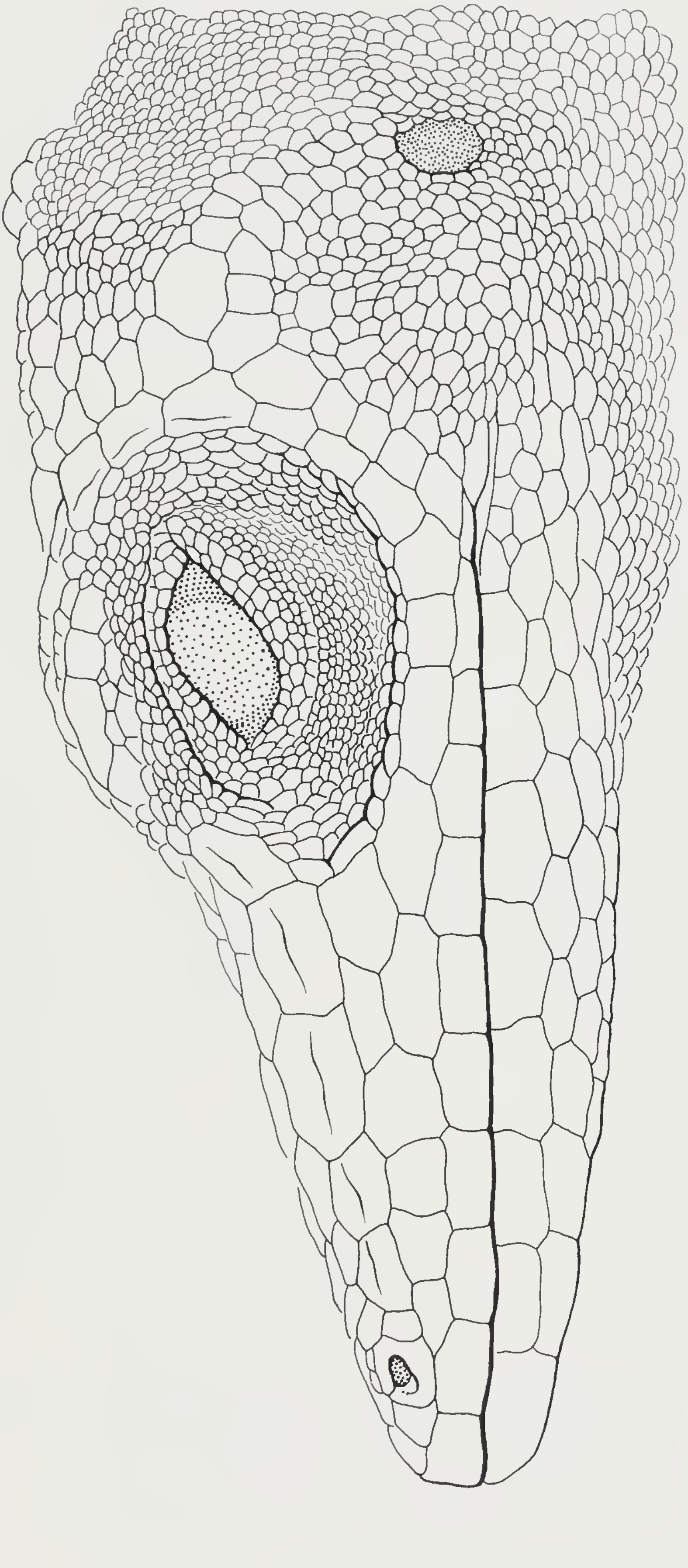

Figure 5. *P. orcesi* Paratype, USNM 166533. Lateral view of head. (Right side reversed.)

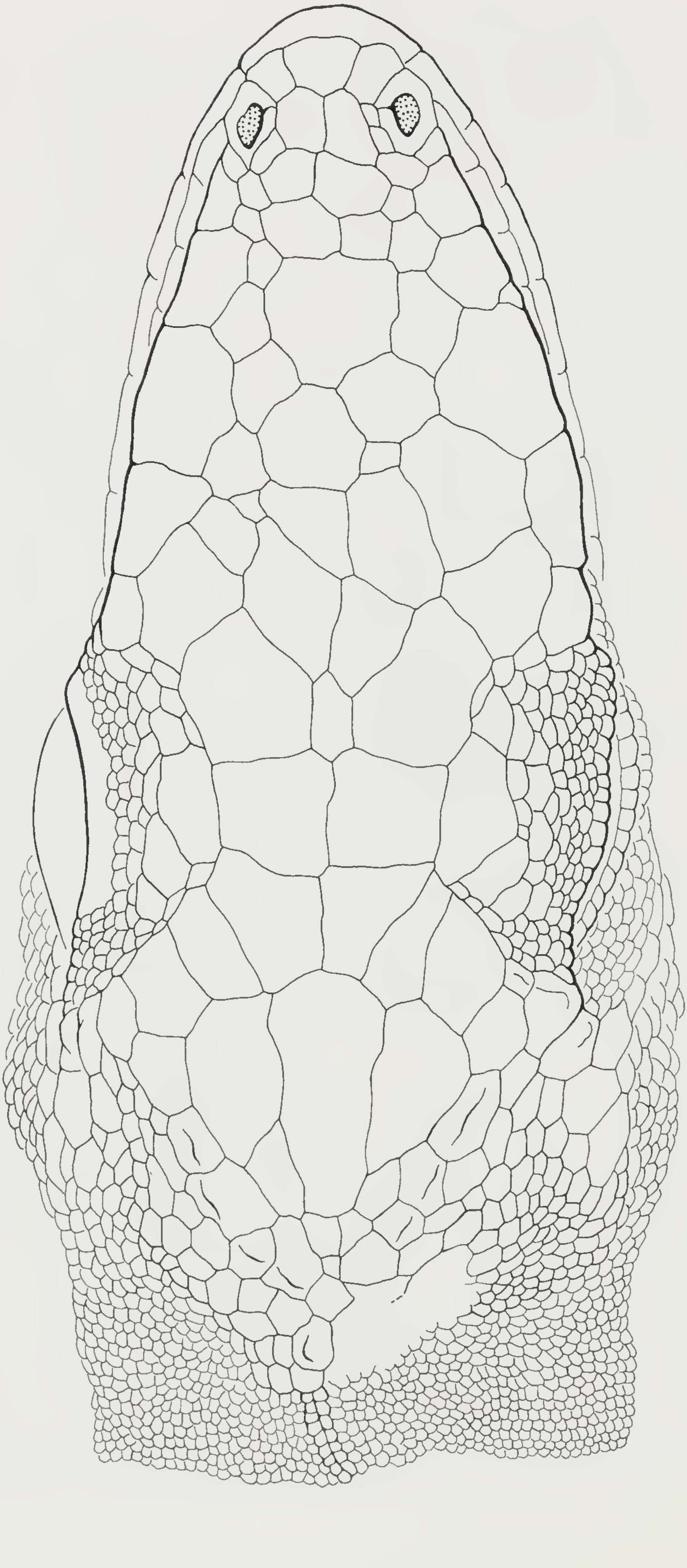

Figure 6. *P. orcesi* Paratype, USNM 166533. Dorsal view of head.

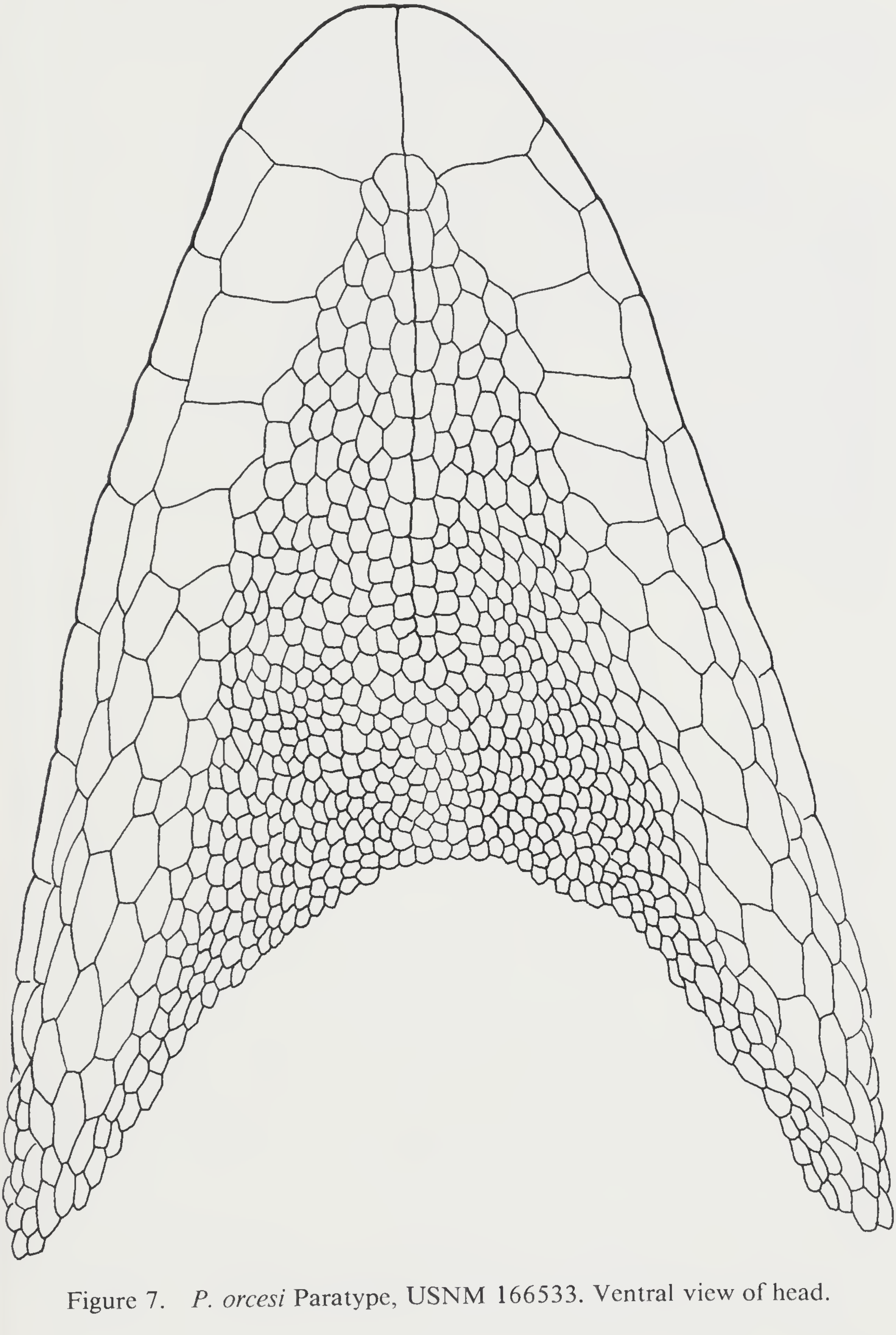

Figure 7. *P. orcesi* Paratype, USNM 166533. Ventral view of head.

Table 1. Comparative scale variations in the Peruvian phenacosaur and *orcesi* and *heterodermus.*

	Peruvian phenacosaur	*orcesi*	57 *heterodermus*
Scales between second canthals	4	4	3–6
Postrostrals	**4**	2–3	3–6
Scales between supraorbital semicircles	0	0	0–1
Scales in supraocular disk	**4**	5–6	1–6
Elongate supraciliaries	**2**	1	0–2
Loreal rows	2–3	2	1–3
Total loreals	**10-11**	6–7	3–12
Scales between interparietal and semicircles	0	0	0–2
Scales between interparietal and nape scales	**5**	4	3–8
Postmentals (including sublabials)	**4**	5–6	2–6
Scale rows in vertebral crest	0	0–1	0–2
Lamellae under phalanges ii and iii fourth toe	**21**	17–19	18–24

not been previously illustrated. (The head and body characters of the type of *P. orcesi* are figured in Lazell, 1969.)

It should be parenthetically mentioned that the issue of the validity or non-validity of the genus *Phenacosaurus* does not arise in the present context. That this Peruvian specimen belongs in the lineage that includes the species *heterodermus* is not, for us, in question. The validity of the genus *Phenacosaurus* depends upon osteological characters not observable in the present specimen and upon hypotheses of the phylogenetic significance of those characters. The placement of the Peruvian animal within the postulated lineage *orcesi, nicefori, heterodermus* depends upon external phenetic resemblances, unknown or very unusual in *Anolis,* that, in our judgment, demonstrate that these species are a clade.

There are seven differences between the juvenile and the two adult *P. orcesi,* none of these such that they could not be ascribed to the sort of individual variation that is rampant in the one well-collected species, *P. heterodermus.* These are in bold face in Table 1, which records counts for the Venceremos juvenile, the two Ecuadorian *orcesi,* and for 57 *heterodermus.* It is clear that variation in these counts exceeds species boundaries. However, cer-

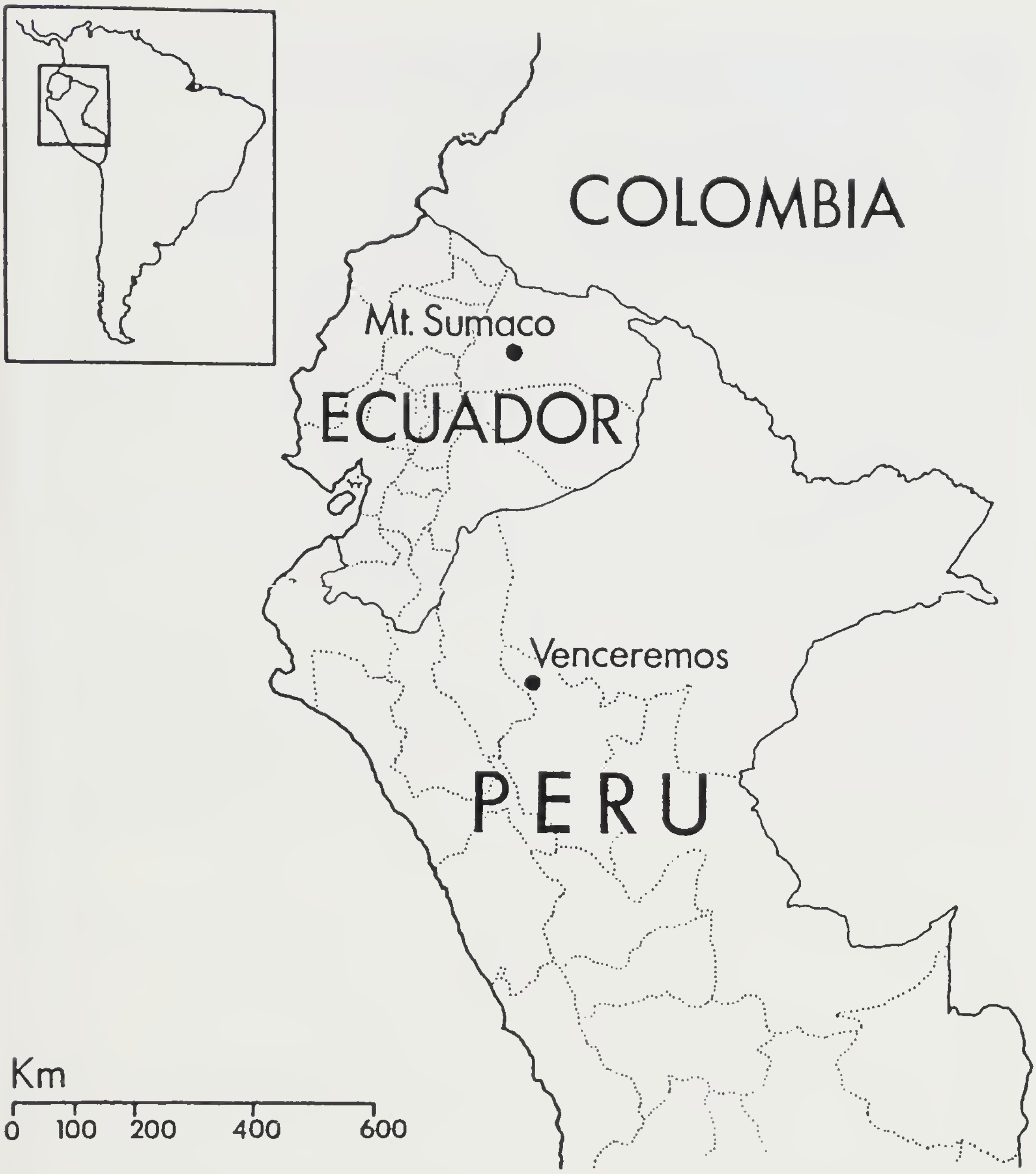

Figure 8. Map showing the Ecuadorian type locality of *P. orcesi* (Mt. Sumaco) and the locality for the Peruvian juvenile (Venceremos).

tain counts generally tend to be associated with body size in anoles; thus the count of 21 for the fourth toe lamellae for the Peruvian juvenile may, possibly, indicate that the adults of this population might be nearer *heterodermus* size (maximum SVL ca. 80 mm) than *orcesi* size (known maximum SVL 67 mm).

There are, therefore, only two reasons for hesitation for recognizing the Peruvian juvenile as *P. orcesi*: (1) the fact that it is a juvenile, and (2) the very considerable range extension (more than 500 km; Fig. 8) from the southernmost (type) locality Mt.

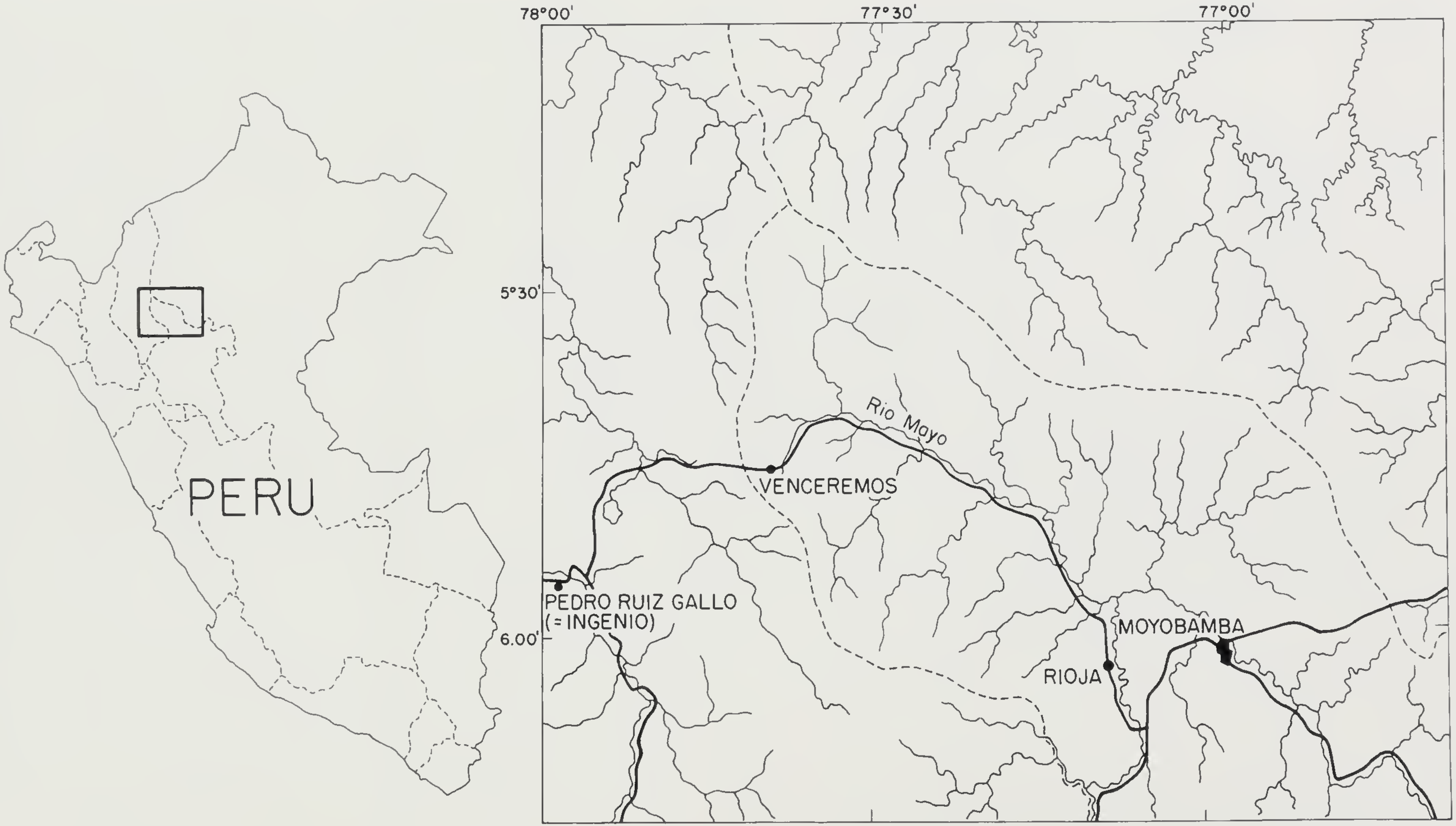
PERU
78°00'
77°30'
77°00'
5°30'
6.00'
Rio Mayo
VENCEREMOS
PEDRO RUIZ GALLO
(= INGENIO)
MOYOBAMBA
RIOJA

Figure 9. Left: Map to show the Venceremos area in relation to Peru as a whole. Right: Detail map to show Venceremos in relation to other localities in northern San Martin and adjacent Amazonas, Peru.

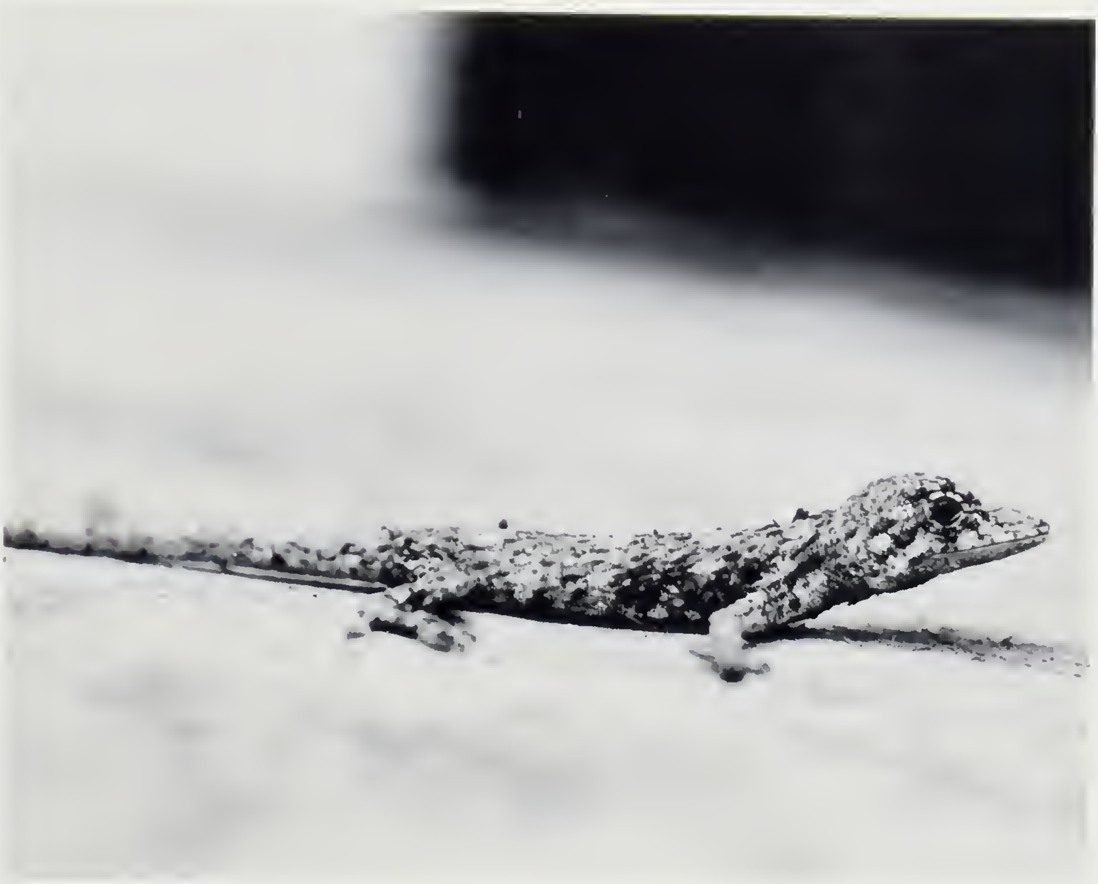

Figure 10. Photograph of the Peruvian phenacosaur in life. Photo by R. A. Mittermeier.

Sumaco, Napo Province, Ecuador (0°34′S, 77°09′W), to Venceremos, Department of San Martin, Peru (ca. 5°45′S, 77°45′W) (see Fig. 9). While *P. orcesi* is quite distinct from *P. heterodermus* and its relatives, *P. nicefori, P. inderenae,* and the undescribed giant species from Ecuador, the latter are a complex in which the species are not very sharply delimited morphologically; it is a possibility that *P. orcesi* is a complex also, and that the Peruvian juvenile is a distinct species. Provisionally we assign the Peruvian specimen (Fig. 10) to the species *P. orcesi,* but new material and much more careful collecting in the montane areas of Peru and Ecuador are clearly much to be desired.

ACKNOWLEDGMENTS

The figures of the phenacosaurs were done by Laszlo Meszoly, the maps by Stephen D. Nash and Laszlo Meszoly.

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NEW *COLOSTETHUS* (AMPHIBIA, DENDROBATIDAE) FROM SOUTH AMERICA

Juan A. Rivero[1]

Abstract. Six new species of *Colostethus* are described from South America: *C. mittermeieri, C. idiomelus,* and *C. poecilonotus* from Peru; *C. maculosus* and *C. paradoxus* from Ecuador; and *C. faciopunctulatus* from Colombia. *C. maculosus* and *C. faciopunctulatus* belong to group VI (Rivero and Serna, 1988), *C. mittermeieri* and *C. idiomelus* to group I, *C. poecilonotus* belongs to group IX, and *C. paradoxus* to group IV.

The relationship of the various species is discussed. *C. poecilonotus* is the first member of group IX described from Peru, while *C. paradoxus* is the second member of group IV known from Ecuador. Group IV only extends south to the latitude of Quevedo in northwestern Ecuador. *C. paradoxus* extends the range of the group to southern Ecuador. However, the possibility that the dilated third finger, which characterizes male members of group IV, may have arisen independently on more than one occasion is discussed.

INTRODUCTION

Examination of the *Colostethus* collection at the Museum of Comparative Zoology revealed a number of undescribed species from Peru, Ecuador, and Colombia. From these undescribed species a great deal is learned regarding their mutual relationships and the delimitation of the groups the genus has been divided into (Rivero, 1988).

All the described species are well characterized and one of them is quite unique, so unique indeed that it cannot easily be assigned to any of the known groups of *Colostethus*. Yet, most of the groups, as originally suggested (Rivero, 1988), seem to have withstood trial, although a few definitions may require modification. The division of the original group VI into groups VI and IX follows Rivero and Serna, 1988. A description in English (expanded from the original in Spanish) of the Andean groups occurring from Colombia to Peru is provided here.

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Many of the proportions usually incorporated into descriptions have been omitted here (diameter of tympanum in relation to eye diameter, diameter of eye in relation to the distance between eye and nostril, etc.) as they can easily be determined from the measurements. When many specimens were available, averages and proportions are provided in a *Variation* section.

Most measurements were taken with a compass; snout–vent length, head breadth, and length of tibiae, with calipers. Head length was measured between the posterior edge of the tympanum and the tip of the snout.

The web between the toes is considered insignificant if it does not extend beyond the midpoint of the first subarticular tubercle in at least four toes, minimal if it extends to the anterior border of the first subarticular tubercle in at least four toes (¼-webbed), intermediate if it extends beyond the first subarticular tubercle but does not reach the last articulation (disk) in at least three toes, and extensive if it reaches the last articulation in at least four toes. The central and usually indented part of the web is the portion considered for determining its extension. Considering the individual variation, a more detailed description is unnecessary and may make comparisons more difficult. However, the pedal membrane of all holotypes is illustrated in the corresponding figures.

The author wants to thank E. E. Williams and J. Rosado for all their courtesies and attentions during his stay at the MCZ.

DEFINITION OF GROUPS

Group I. Two pectoral spots present, dorsolateral and ventrolateral stripes absent; oblique-lateral stripes present and usually complete (from eye to groin), rarely absent; pedal membrane absent or insignificant, rarely extensive; third finger of males not dilated; cloacal funnel absent.

Group II. Dorsolateral stripes present; oblique-lateral stripes absent or incomplete (not reaching the eye); ventrolateral stripes present or absent; pedal membrane absent or insignificant; paired pectoral spots absent; third finger of male not dilated; cloacal funnel absent.

Group IV. Third finger of males dilated; dorsolateral stripes usually absent; oblique-lateral stripe present or absent; ventrolateral stripe generally absent; pedal membrane absent or insignificant (except in Colombian *C. agilis*); paired pectoral spots absent; cloacal funnel absent.

Group V. Cloacal funnel present; dorsolateral stripe absent or indistinct; oblique-lateral stripe absent; ventrolateral stripe absent; pedal membrane extensive; paired pectoral spots absent; third finger of male not dilated.

Group VI. Pedal membrane usually extensive, at least ⅓ the length of the toes; first finger generally shorter than second; dorsal color usually blackish, sometimes marbled or spotted; dorsolateral stripes absent or not extending posteriorly beyond sacral hump; oblique-lateral stripes absent or incomplete; ventrolateral stripes generally absent; paired pectoral spots absent; third finger of male not dilated; cloacal funnel absent.

Group IX. Dorsolateral stripes absent; oblique-lateral stripes present and usually complete (from eye to groin); ventrolateral stripes generally absent; pedal membrane absent or insignificant; paired pectoral spots absent; third finger of male not dilated (this last character distinguishes this group from group IV); cloacal funnel absent.

DESCRIPTION OF SPECIES

Colostethus mittermeieri, sp. nov.

Figs. 1a–d

Holotype. MCZ-A 100217, an adult female from Venceremos, 394–395 km, on Marginal de la Selva Road, 1,620 m, Departamento de San Martín, Perú. Collectors: R. A. Mittermeier and H. Macedo Ruíz, 26 Sept. 1978.

Paratypes. MCZ-A 100218–57. Forty specimens with the same data as the type.

Etymology. Mittermeieri, in honor of Russell A. Mittermeier, one of the collectors of the species, and recent recipient of the N.Y. Zoological Society's Conservation Medal.

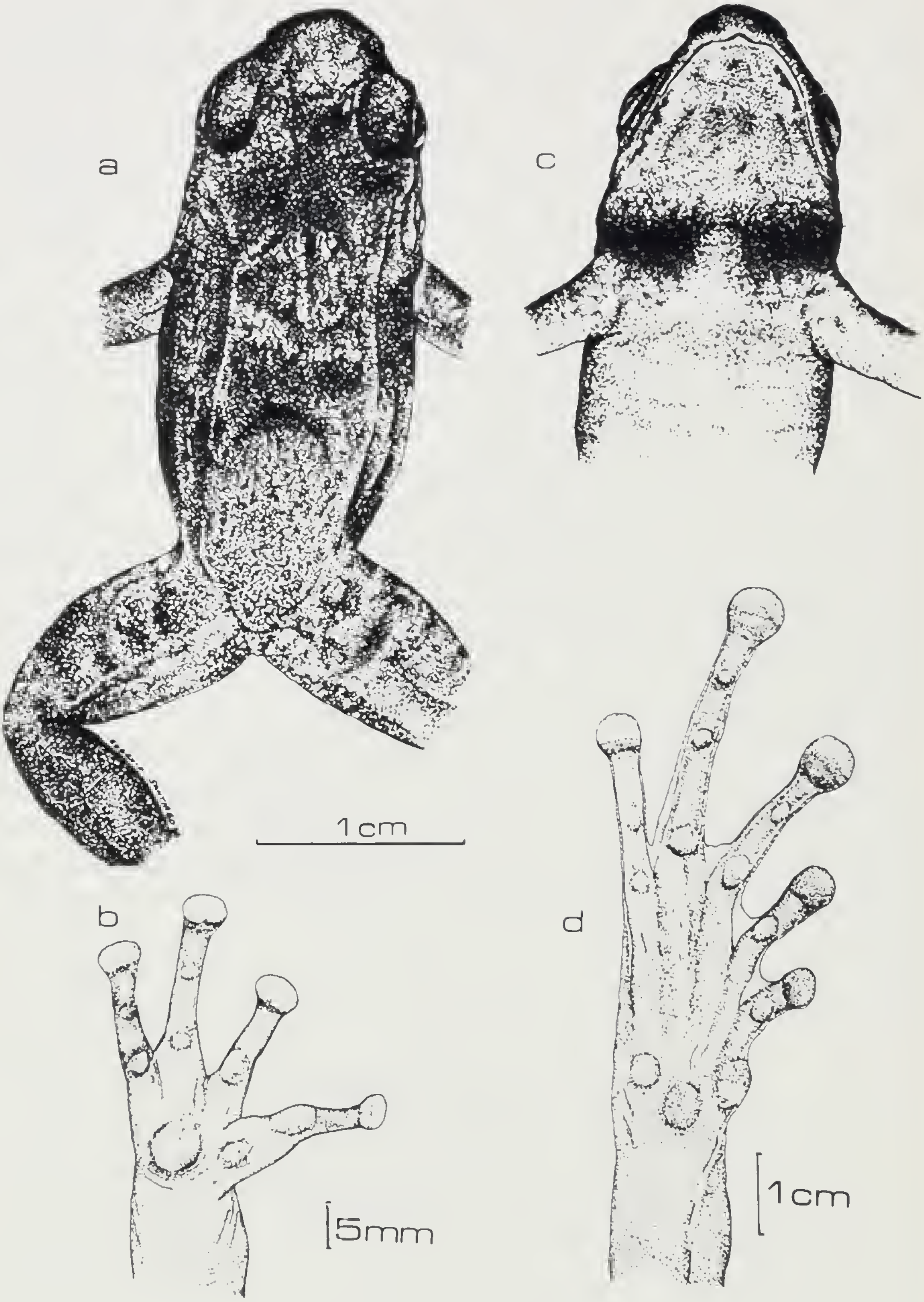

Figure 1. MCZ-A 100217, holotype of *Colostethus mittermeieri,* (a) dorsal view; (b) ventral view of hand; (c) throat and chest; (d) ventral view of foot.

Diagnosis. A fairly large member of group I (Rivero, 1988) with ¼-webbed toes, first finger shorter than second, fingers without lateral fringes, toes with distinct lateral fringes, venter almost always marbled, especially on the anterior half, males without vocal slits, no ventral sexual dichromatism, flanks with contrasting and sometimes elongated spots, digital disks broader than distal segments, and no dorsolateral, oblique-lateral, or continuous and distinct ventrolateral stripe.

Description of Holotype. Tip of snout broadly triangular beyond nostrils, almost vertical when seen from the side; nostrils anterolateral, slightly protuberant; tongue spatulate, nicked behind, about ⅔ free; choanae rounded; canthus rostralis well defined, angular, curved; loreal region flat, vertical; tympanum moderate, covered posterodorsally by skin; external metacarpal tubercle rounded, prominent; internal tubercle elongate, prominent; palm of hand smooth, with a slight ridge along outer margin; proximal subarticular tubercles of first two fingers large, prominent; proximal of outer two fingers smaller, less distinct; distal of outer two fingers reduced, inconspicuous; first finger shorter than second, second shorter than last; fingers without lateral fringes; disks large, broader than distal digital segments; first disk slightly smaller than second and fourth; third disk about ¾ size of tympanum; a distinct, oblique tarsal fold extending to inner subarticular tubercle; three metatarsal tubercles, inner more elongated, central less prominent, than outer; plantar surfaces smooth, with a distinct ridge along outer margin; toes with a minimal web; toe disks broader than distal digital segments; first disk smaller than others; all toes with distinct lateral fringes; heel of adpressed hind limb extending anteriorly to middle of eye.

Head smooth; dorsal surfaces behind head covered with flat, minute warts sometimes fusing to form short ridges; a few tubercles behind sacral hump, in the proximity of cloacal opening; two or three tubercles between tympanum and arm; flanks with small, flat warts and glandular ridges; loreal region smooth; a few tubercles on dorsal surface of arms and a few others on anteroventral surfaces of upper arm; venter smooth except for some indistinct granules on the posterior lateral margins of abdomen; ventral surface of thighs smooth.

Color. Dorsum solid dark grayish brown; loreal region, upper lip and temporal area lighter than dorsum; flanks the same color as dorsum but with a few distinct white spots near groin and a white streak that extends from axilla to ⅔ distance from axilla to groin; white streak shorter and not extending to axilla on left side; a white or discolored area at attachment of forelimb; black longitudinal streaks along anterior and posterior aspects of forearms or thighs absent; posterior aspect of thighs with indistinct blackish marbling on a greenish yellow background; dorsal aspect of thigh with indistinct transverse blotches or bars.

Throat and anterior part of belly infuscated, this color more concentrated on throat and chest, with two extensive black spots discernible; sides of belly with some infuscation and marbling; dorsolateral, continuous ventrolateral, and oblique-lateral stripes absent; a few indistinct whitish spots or bars on anterior aspect of thighs.

Variation. Almost always the dorsal color of adults is solid dark grayish brown or blackish, but it may be lighter gray in an occasional specimen, and indistinct darker spots may be discerned in some specimens, particularly the young ones. Transverse bars on the limbs may also be distinct in juveniles but are rarely so in adults.

The white spots of the flanks may vary in distinctness and may not be apparent in some juveniles. The ventrolateral streak may be continuous between groin and axilla, it may be broken into a series of longitudinal spots, or it may be limited to a few anterior spots. It never has either the smooth margins or the continuity of the ventrolateral streak in members of groups II and IV, nor does it extend anteriorly beyond the origin of the arm. The discolored area at the attachment of the forelimb is present in most specimens but is not apparent in those in which the limbs are of a light color.

A marbled and spotted ventral pattern may not be apparent in a few specimens (N5) but it is usually present. Infuscation of the throat and chest is generally present, but again, an occasional specimen may be of a plain white color, except for the two spots on the chest. In some specimens with a distinct marbled pattern on the anterior venter, the knee may also be marbled and/or spotted.

The white spots on the anterior aspect of the thigh may be quite distinct, and in some specimens there is a row of white spots along the posterior margin of the thigh and tibial segment.

In one female specimen, the dorsum is quite tubercular; in others there are small tubercles on the anterolateral area of the dorsum. The indistinct warts and rugosities of the dorsum are generally present but may be absent in young individuals. In the latter the disks are not usually broader than the distal digital segments.

There is some slight variation in the amount of webbing, especially of the first finger, which may be from fully webbed to about half-webbed.

The tubercles on the forearm may be quite abundant and distributed all along the anterior and posterior surfaces, or limited to a few, which form an irregular row on the posterior face of the arm. The belly is usually smooth, but a few specimens have granules on the distal third of the belly, on the sides, and/or on the ventral surface of the thighs.

None of the 10 recognizable males in the group is larger than 20 mm and none has vocal slits. The latter characteristics may be a sign of immaturity; however, these specimens' testicles seem to be well developed. There may be a distinct size dimorphism in this species.

Measurements and Proportions. See Tables 1a and 1b.

Discussion. Colostethus mittermeieri is a member of group I, whose most distinctive feature is the presence of two dark pectoral spots.

Group I has 12 species, six of which are yet to be described (Edwards, 1974; Rivero, 1988). The group ranges from southern Colombia to Peru south to Cerro de Pasco. In the Peruvian Andes it is the dominant group and the only one in their highest elevations, but it occurs, as do groups VI and II, on the eastern flank of the cordillera.

The only member of group I so far known from the lowland is *C. littoralis,* described from Lima, but this form is apparently identical with a species from Ancash and may have been taken to the coast, either intentionally or accidentally. The small coastal population seems to have disappeared now but the name *C. littoralis* prevails for the mountain form.

Table 1a. *Colostethus mittermeieri* males, measurements and proportions.

Catalog No.	100228	100224	100233	Average
SV	19.00	17.45	15.30	17.25
HB	6.65	6.20	5.40	6.08
HL	7.70	6.30	5.50	6.50
ETS	3.60	3.35	2.80	3.25
EN	1.95	1.70	1.80	1.82
IOS	2.10	2.30	2.05	2.15
UE	1.80	1.60	1.50	1.63
ED	2.80	2.45	2.50	2.58
DT	1.20	0.95	1.20	1.12
LF	8.70	7.90	7.20	7.93
LT	8.90	8.30	7.35	8.18
LFT	8.70	7.60	6.50	7.60
HB/SV	0.35	0.36	0.35	0.35
HL/SV	0.41	0.36	0.36	0.38
UE/IOS	0.86	0.70	0.73	0.76
DT/ED	0.43	0.39	0.48	0.43
ED/ETS	0.78	0.73	0.89	0.80
ED/EN	1.44	1.44	1.39	1.42
LF/SV	0.46	0.45	0.47	0.46
LT/SV	0.47	0.48	0.48	0.47
LFT/SV	0.46	0.44	0.42	0.44
LF/LT	0.98	0.95	0.98	0.97

Key: SV = snout–vent length; HB = head breadth; HL = head length; ETS = distance between eye and tip of snout; EN = distance between eye and nostril; IOS = breadth of interorbital space; UE = breadth of upper eyelid; ED = eye diameter; DT = tympanic diameter; LF = length of femur; LT = length of tibia; LFT = length of foot.

C. mittermeieri is distinguished from all other members of the group, with the exception of an undescribed species from Dos Ríos in Pichinga, Ecuador, by lacking an oblique-lateral stripe. It is also the most extensively webbed species, as in all the others the toes are either free or have an insignificant web.

Most of the Peruvian members of group I are distinctly spotted above. *C. mittermeieri* is not usually spotted, but when spotted, the spots are not distinct and contrasting. On the other hand, the white lateral spots are usually distinct and very contrasting, and one of the lower ones may form a usually discontinuous, undu-

Table 1b. *Colostethus mittermeieri* females, measurements and proportions.

Catalog No.	100234	100250	100256	100249	100247	100217	100244	100229	100242	100257	100245	100241	Average
SV	24.70	29.25	23.50	28.00	27.50	28.00	19.35	28.00	23.00	27.80	20.20	21.00	25.03
HB	8.50	9.50	8.25	9.50	8.70	9.50	7.00	9.00	7.80	9.25	7.10	7.65	8.48
HL	8.30	8.75	8.10	10.50	9.25	9.30	6.90	10.30	8.75	9.75	7.30	7.90	8.76
ETS	4.00	4.40	3.70	4.60	4.45	4.20	3.30	4.50	4.00	4.00	3.40	3.50	4.00
EN	2.40	2.70	2.35	2.40	2.50	2.50	1.80	2.50	2.55	2.50	2.00	2.25	2.37
IOS	3.30	3.25	2.75	3.00	3.15	3.25	2.50	3.20	2.65	3.40	2.40	2.40	2.94
UE	2.35	2.60	2.25	2.50	2.50	2.55	2.00	2.45	2.25	2.60	2.00	2.05	2.34
ED	3.15	3.85	3.35	4.00	3.70	3.65	3.10	3.55	3.35	3.75	3.05	3.30	3.48
DT	1.25	1.85	1.25	1.75	1.50	1.70	1.20	1.65	1.50	1.75	1.15	1.30	1.49
LF	11.65	12.90	10.90	13.00	11.60	13.40	9.50	12.95	10.10	13.00	9.30	10.05	11.53
LT	12.15	13.40	11.60	13.35	13.75	12.90	10.00	13.45	11.80	14.10	10.25	11.10	12.32
LFT	11.30	12.65	10.40	12.75	11.90	12.00	8.55	11.35	10.65	12.35	9.40	10.95	11.19
HB/SV	0.34	0.32	0.35	0.34	0.32	0.34	0.36	0.32	0.34	0.33	0.35	0.36	0.34
HL/SV	0.34	0.30	0.34	0.38	0.34	0.33	0.36	0.37	0.38	0.35	0.36	0.38	0.35
UE/IOS	0.71	0.80	0.82	0.83	0.79	0.78	0.80	0.77	0.85	0.76	0.83	0.85	0.80
DT/ED	0.40	0.48	0.37	0.44	0.41	0.47	0.39	0.46	0.45	0.47	0.38	0.39	0.42
ED/ETS	0.79	0.88	0.91	0.87	0.83	0.87	0.94	0.79	0.84	0.94	0.90	0.94	0.87
ED/EN	1.31	1.43	1.43	1.67	1.48	1.46	1.72	1.42	1.31	1.50	1.53	1.47	1.48
LF/SV	0.47	0.44	0.46	0.46	0.42	0.48	0.49	0.46	0.44	0.47	0.46	0.48	0.46
LT/SV	0.49	0.46	0.49	0.48	0.50	0.46	0.52	0.48	0.51	0.51	0.51	0.53	0.49
LFT/SV	0.46	0.43	0.44	0.46	0.43	0.43	0.44	0.41	0.46	0.44	0.47	0.52	0.45
LF/LT	0.96	0.96	0.94	0.97	0.84	1.04	0.95	0.96	0.86	0.92	0.91	0.91	0.94

For key to characters see Table 1a.

lating line from the axilla to the proximity of the groin. The streak may not be analogous to the ventrolateral streak of groups II and IV.

Colostethus idiomelus, sp. nov.

Figs. 2a–c

Holotype. MCZ-A 100260, an adult female from Venceremos, 394–395 km, on Marginal de la Selva Road, 1,620 m, Departamento de San Martín, Perú. Collectors: R. A. Mittermeier and H. Macedo Ruíz, 26 Sept. 1978.

Etymology. Idiomelus, from the Greek *idio,* distinct, peculiar, and *melos,* limb, in reference to the strikingly colored hind limbs of the species.

Diagnosis. A medium-sized member of group I with small pectoral spots, no dorsolateral or ventrolateral stripes, oblique-lateral stripe present and extending to the eye, first finger shorter than second, a short basal web between toes I and II, and II and III, a narrow lateral fringe on the inner side of toes II and III, fingers and toes long and slender, the disks small, much smaller than the tympanum, and the thighs with distinct transverse blotches on a white background.

Description of Holotype. Snout short, the tip rounded, more or less vertical when seen from the side; nostrils anterolateral, not protruding, very near end of snout; tongue spatulate, broad, nicked behind, about ⅔ free; choanae small, ovate; canthus rostralis rounded but angular, not appreciably curved; loreal region vertical, flat; tympanum flushed with surface, covered posterodorsally by skin; external metacarpal tubercle rounded, obliquely ridged; internal tubercle smaller, elongate; palm of hand smooth, with a narrow ridge along outer margin; basal subarticular tubercles of fingers I, II, and III large, distinct; distal tubercle of finger III and basal and distal tubercles of finger IV smaller and less distinct; fingers long, slender; first finger slightly shorter than second, second shorter than last; fingers without lateral fringes; disks small, approximately equal in size and slightly broader than distal digital segments; disk of third finger about ⅓ size of tympanum; an oblique, internal tarsal fold extending to inner metatarsal tubercle; metatarsal tubercles prominent; outer tubercle more or less rounded; inner, elongate; plantar surfaces smooth and with

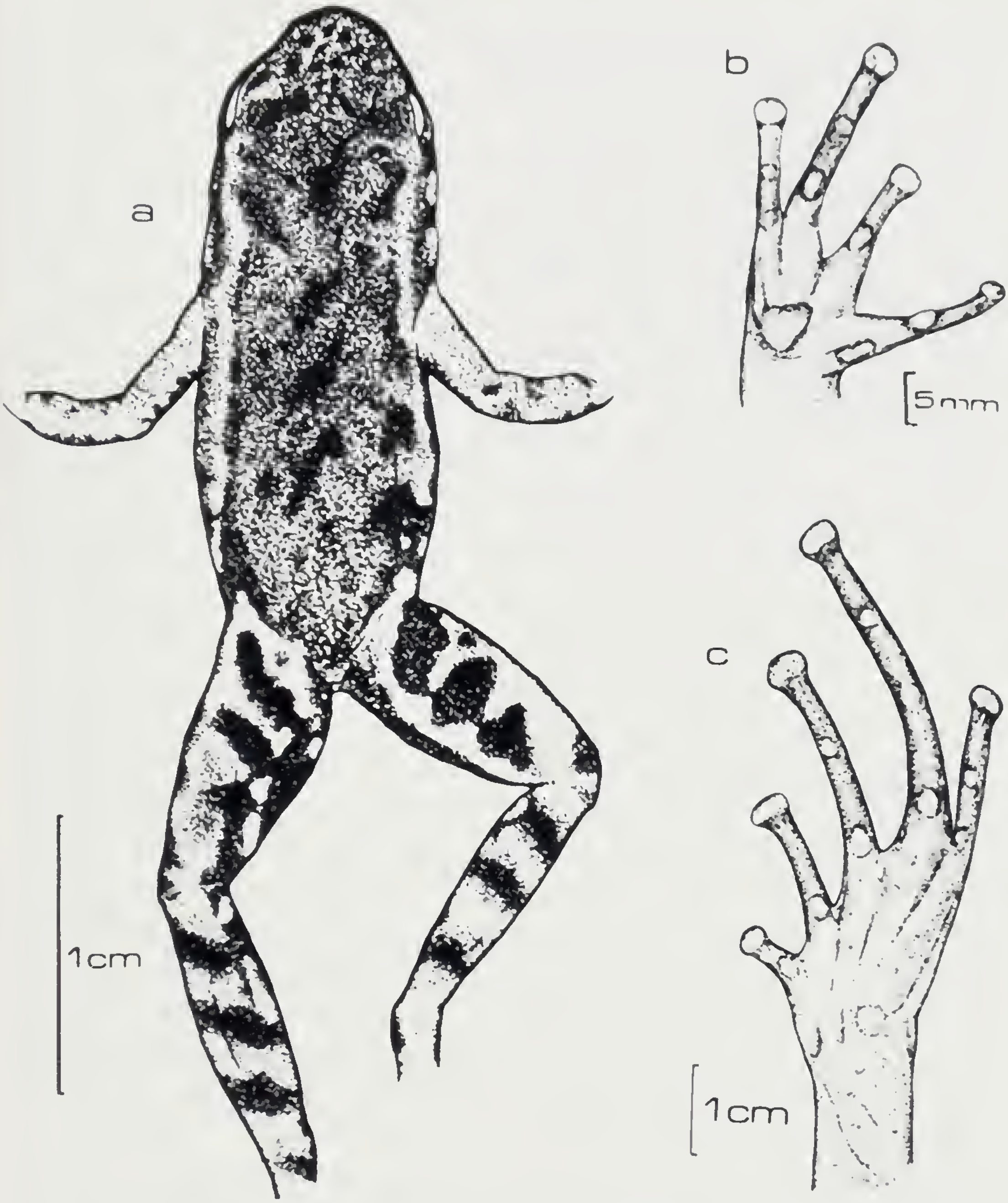

Figure 2. MCZ-A 100260, holotype of *Colostethus idiomelus*, (a) dorsal view; (b) ventral view of hand; (c) ventral view of foot.

distinct outer ridge extending as narrow keel along outer edge of fifth toe; toes slender, with insignificant web; disks of toes small; first disk not broader than digit; others slightly broader; heel of adpressed hind limb extending anteriorly to middle of eye.

Dorsum smooth on head and anterior part of body but with indistinct flat warts increasing in size near cloacal opening; loreal region and flanks smooth; a tubercle between tympanum and arm;

three or four small tubercles along posterior surface of lower arm; ventral surfaces, including posterior surface of thighs, smooth.

Color. Dorsum grayish brown with moderately contrasting blotches and spots which are much smaller on snout and head; a black streak on each side, from behind eye, crossing groin area and continuing along anterior border of thigh to knee; an oblique, white (red?) stripe crossing base of thighs and on one side continuing as a longitudinal stripe along posterodorsal margin, on other, breaking into a series of spots; anterior part of thighs white, this color getting dusky at fusion with white streak or spots on posterodorsal margin; white or whitish area crossed by three very distinct and contrasting dark brown spots or bars; posterior part of thighs behind white streak (or series of spots) dark brown, lighter and profusely spotted with white at proximal end; rest of hind limbs light brown with darker crossbands; a short dark brown streak on anterior part of upper arm and a longer one on posterior portion of same segment; a small, dark brown spot around nostril; a dark canthal streak continuing to tip of snout but not meeting contralateral streak; exposed part of tympanum white; upper lip and temporal area dusky, with spots below anterior and posterior corners of eye and smaller spots between these and below canthal streak; a whitish oblique-lateral stripe from behind eye to proximity of groin; groin area very dark brown, with distinct and contrasting white spots, one of which extending into white, oblique streak at base of thighs; the brown color, on the other hand, extending into black streak along anterior aspect of thighs; ventral surfaces immaculate except for a dusky line along margin of lower jaw and two tiny pectoral spots.

Measurements (mm). Snout–vent 25.3; head length 8.2; head breadth 8.1; eye diameter 3.0; eye–nostril 2.0; eye–tip of snout 4.0; upper eyelid 2.0; interorbital space 3.0; femur 12.0; tibia 12.2; foot 12.5.

Discussion. Colostethus idiomelus shares with most of the other Peruvian members of group I the oblique lateral stripe and the spotted coloration of the dorsum. *Colostethus sylvaticus, C. elachyhistus,* and *C. littoralis,* the other described members of group I, have a greater amount of webbing and a distinct lateral fringe on all toes. None has the striking coloration of the thighs nor the white spots on the flank that seem to characterize *C. idiomelus.*

Two undescribed species were considered by Edwards in his thesis (1974). In one, from Ancash, there is no pedal webbing and the oblique-lateral line does not extend to the eye; in the other, from Huánuco, fingers and toes are fringed, the flanks are dark brown, with a number of yellowish flecks and the dorsal surfaces of the limbs are olive tan with brown bars or spots.

A third species collected by Edwards near Zamora in Ecuador, but not yet described, has a yellow spot at the insertion of the arm and brown legs with small black spots and transverse bars.

Colostethus idiomelus is more typical of group I than *C. mittermeieri.* It differs from that species, among other things, in having black streaks along the anterior and posterior aspect of the upper arms, in having a reduced amount of webbing, no blackening of the throat, very small pectoral spots, and an oblique-lateral streak.

Colostethus poecilonotus, sp. nov.

Figs. 3a–c

Holotype. MCZ-A 89108, an adult female from between Chachapoyas and Bagua Grande Alva, 500 m, Departamento Amazonas, Perú. Collector: R. A. Mittermeier, 3 May 1974.

Paratypes. MCZ-A 89106–7, 89109, all adults and with the same data as the type.

Etymology. Poecilonotus, from the Greek *poikilos,* variegated, spotted, mottled, and *notos,* back, in reference to the spotted dorsum of this species.

Diagnosis. A small *Colostethus* probably belonging to group IX, with granular, spotted dorsum, no dorsolateral or ventrolateral stripes, oblique-lateral stripe present and not extending beyond level of axilla, first finger equal in length to second, fingers without lateral fringes, toes free and without lateral fringes, first and fifth toe disks scarcely broader than the respective distal digital segments, venter immaculate, granular on the posterior portion.

Description of Holotype. Tip of snout slightly convex beyond nostrils and slightly inclined inwards towards lip when seen from the side; nostrils anterolateral, slightly protruding; tongue spatulate, entire, ⅔ free; choanae small, rounded; canthus rostralis sharp and angular, curving towards nostrils; loreal region flat, vertical; tympanum conspicuous, posterodorsally covered by skin;

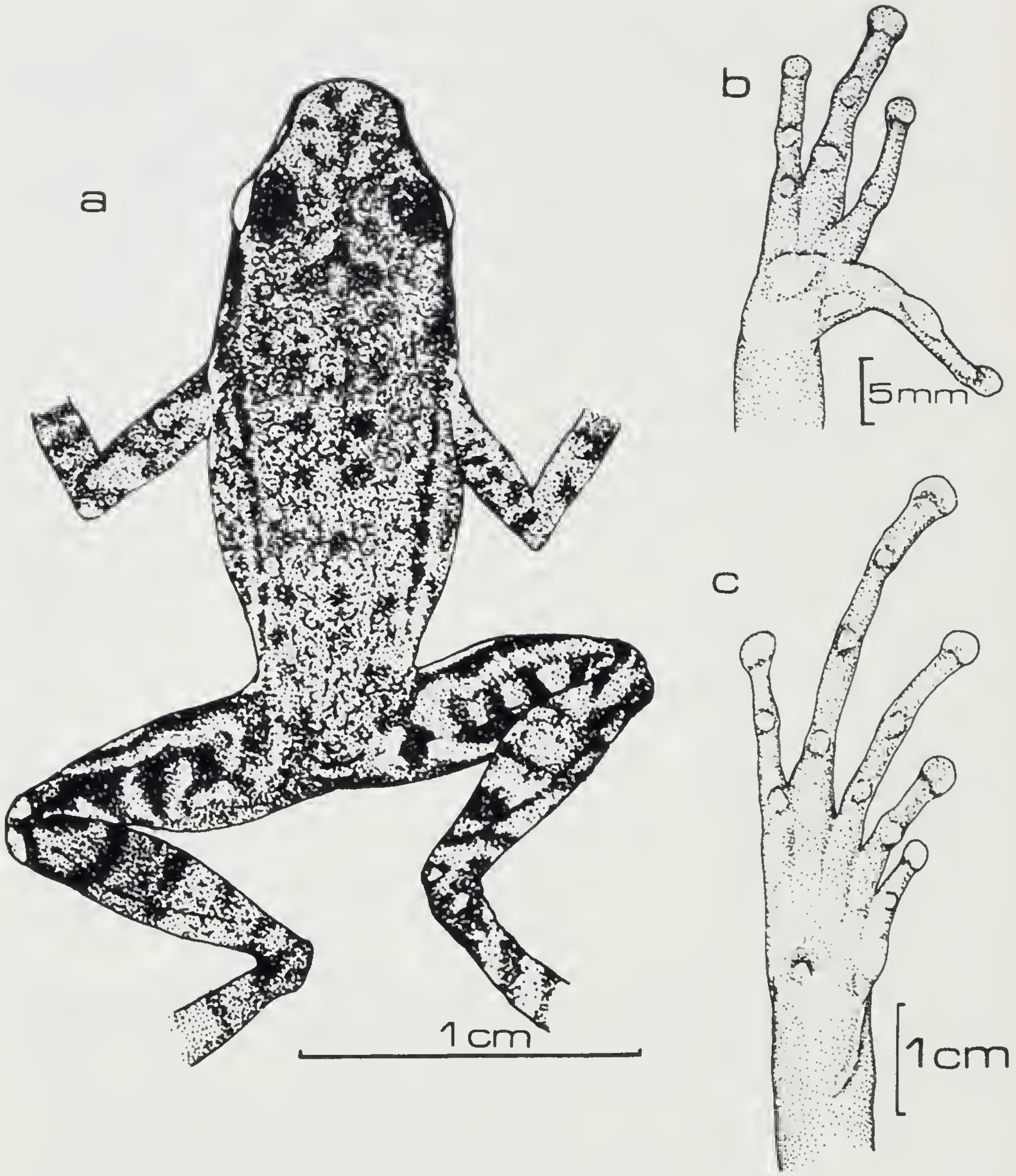

Figure 3. MCZ-A 89108, holotype of *Colostethus poecilonotus,* (a) dorsal view; (b) ventral view of hand; (c) ventral view of foot.

external metacarpal tubercle rounded, very protuberant; inner tubercle elongated and smaller; palm of hand rugose but without supernumerary tubercles and with a ridge along outer margin; subarticular tubercles prominent, the second of third finger and the two of fourth, the smallest (with the latter more prominent than the former); first finger equal in length to second, second slightly longer than last; fingers slender and without lateral fringes; disks of fingers small, all of approximately equal size and slightly broader than corresponding digital segments; disk of third finger not more than ¼ size of tympanum; a short, oblique tarsal tubercle extending as a thin, inconspicuous ridge to inner metatarsal tubercle; inner metatarsal tubercle elongate, longer than the smaller, rounded, and conical outer tubercle; plantar surfaces smooth and with a narrow external fold extending along outer margin of fifth toe to disk; subarticular tubercles of toes small, but conical and protuberant; toes long and slender, free; fourth toe with narrow, indistinct lateral keels on outer segments; first and last disks the smallest and not broader than the corresponding distal digital segments; heel of adpressed hind limb extending anteriorly to between eye and nostril.

Dorsum granular, the granules tending to be more prominent towards posterior end; limbs granular and tubercular; upper eyelids granular; loreal region smooth; flanks granular and tubercular, especially towards groin; two small tubercles between tympanum and arm; throat smooth; abdomen granular on posterior third; posterior aspect of thighs smooth; two or three tubercles along anterior margin of lower arm.

Color. Brownish tan with distinct, darker spots and a distinct whitish oblique-lateral stripe from level of axilla to groin; a black canthal stripe continuing, in back of eye, to about level of arm insertion, after which, continuing posteriorly as a thin stripe above oblique-lateral stripe to groin; upper flanks brownish, with two or three whitish spots near groin; face, lower part of tympanum, and temporal area whitish, this color continuing above arm insertion to lower flanks; an indistinct, brown longitudinal line along anterior face of upper arm and also along anterior face of thighs; hind limbs with narrow cross-bars and spots; posterior aspect of thighs approximately of same color as dorsal surfaces; venter immaculate.

Variation. Paratype MCZ-A 89109 is very similar to the type in coloration, but the black streak above the oblique-lateral line is not easily discernible, the longitudinal line of the upper arm is very short, there are no white spots on the posterior aspect of the flanks, and all disks are broader than the respective digital segments.

In MCZ-A 89107 the dorsal spotting is less contrasting, the loreal region and face are more infuscated or spotted, and the

Table 2. *Colostethus poecilonotus* females, measurements and proportions.

Catalog No.	89106	89107	89108	89109	Average
SV	21.70	24.65	20.50	19.70	21.64
HB	7.20	7.65	7.00	6.20	7.01
HL	8.80	9.45	8.35	7.60	8.55
ETS	3.80	3.85	3.65	3.35	3.66
EN	2.10	2.20	2.10	1.85	2.06
IOS	2.75	3.00	2.80	3.90	2.86
UE	1.85	1.90	1.55	1.40	1.68
ED	3.00	3.20	2.95	2.80	2.99
DT	1.50	1.70	1.45	1.40	1.51
LF	9.80	10.30	9.80	8.90	9.70
LT	10.85	11.05	10.80	9.55	10.56
LFT	10.10	10.00	10.10	9.00	9.80
HB/SV	0.33	0.31	0.34	0.31	0.32
HL/SV	0.41	0.38	0.41	0.39	0.40
UE/IOS	0.67	0.63	0.55	0.48	0.59
DT/ED	0.50	0.53	0.49	0.50	0.51
ED/ETS	0.79	0.83	0.81	0.84	0.82
ED/EN	1.43	1.45	1.40	1.51	1.45
LF/SV	0.45	0.42	0.48	0.45	0.45
LT/SV	0.50	0.45	0.53	0.48	0.49
LFT/SV	0.47	0.41	0.49	0.46	0.46
LF/LT	0.90	0.93	0.91	0.93	0.92

For key to characters see Table 1a.

dark lateral band is broad and has the oblique-lateral line within its confines. The dorsum of this specimen is more tubercular than in the type and there is a central tubercle between inner and outer metatarsal tubercles.

In MCZ-A 89106 there is more spotting on the flanks and some marbling behind the axilla. In both this specimen and MCZ-A 89107 the thighs are marbled dark brown on a lighter brown color.

In most specimens, the oblique-lateral line tends to become whiter, broader, and more distinct as it approaches the groin, and the elbow, the knee, and the heel tend to show a discolored area or spot, but it could not be ascertained if this was the result of erosion or if it is a natural spot.

The lateral keels on the distal segments of the fourth toe are not evident in some specimens and cannot be described as fringes.

Measurements and Proportions. See Table 2.

Discussion. Colostethus poecilonotus is the first member of group IX described from Peru. Yet, its presence here is not unexpected as the group is known from southeastern Ecuador, where it is represented by at least three species. One of these, *C. festae* is little known but it is supposed to have a short web and no oblique-lateral stripe. The others, reported by Edwards (1974) but not yet described, may have a web, fringes on the toes, or a marbled venter.

Sometimes, individuals of species belonging to group I may not have the pectoral spots that are diagnostic of the group. Thus, *C. poecilonotus* may actually be a member of group I, which is the most typical group in Andean Peru. There is no way of knowing, however, until more specimens become available.

Only one undescribed member of group I reported from Peru (Edwards, 1974) lacks toe webbing, but in this species there are fringes on the fingers and toes, and the first finger is longer than the second.

Colostethus maculosus, sp. nov.

Figs. 4a–c

Holotype. MCZ-A 91558, an adult male from Puyo, between Turingia and theatre, 950 m, Provincia Pastaza, Ecuador. Collectors: K. Miyata and H. Weed, 22 July 1976.

Paratype. MCZ-A 104946, an adult male from El Reventador (ca. 1,200 m), Provincia Napo, Ecuador. Collector: Giovanni Onore, Leg. June, 1983.

Etymology. Maculosus, from the Latin *maculosus,* spotted, mottled, in reference to the color of the dorsum in this species.

Diagnosis. A medium-size *Colostethus* referable to group VI, with mostly smooth and spotted dorsum, first finger shorter than second and second much shorter than fourth, vesicular inflammation at base of third finger, extensively webbed toes, no dorsolateral or ventrolateral stripes, but variously distinct, oblique-lateral line present, black lateral band not extending posteriorly behind arm, and immaculate venter.

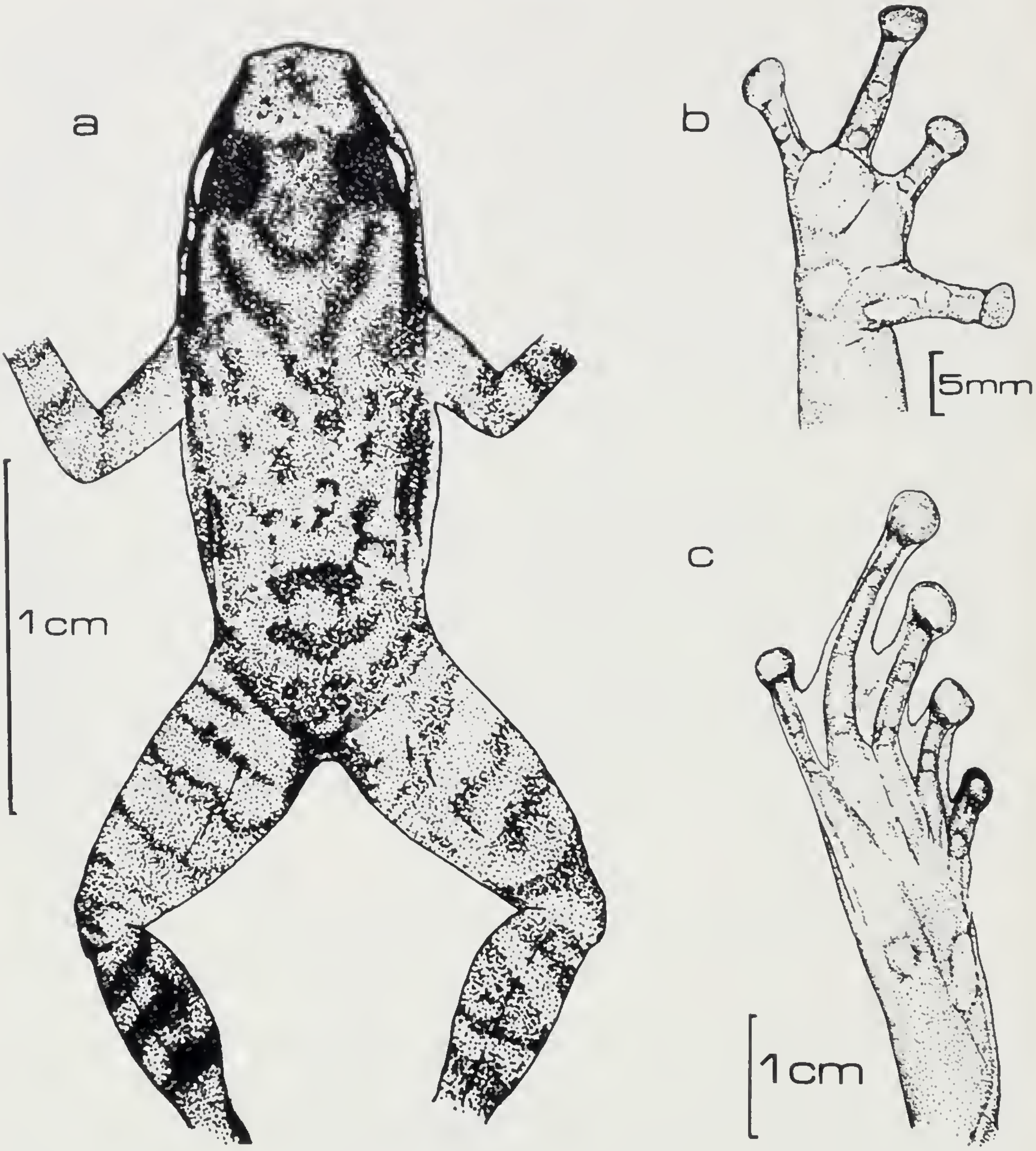

Figure 4. MCZ-A 91558, holotype of *Colostethus maculosus,* (a) dorsal view; (b) ventral view of hand; (c) ventral view of foot.

Description of Holotype. Tip of snout almost truncate, slightly inclined inwards towards the lip when seen from the side; nostrils anterodorsal, scarcely protruding; tongue narrow, ovoid, nicked behind, and nearly ½ free; choanae small, rounded; canthus rostralis sharply angular; loreal region vertical, flat; tympanum moderate, covered posterodorsally by skin; external metacarpal tubercle large, rounded, protuberant; internal tubercle smaller, elongate, and less prominent; palm of hand smooth, with a distinct pad or cushion at base of third finger; an indistinct outer ridge along outer margin of hand; subarticular tubercles rather small, the ones in outer finger the smallest; first finger much shorter than second, second considerably shorter than fourth; fingers flat, without lateral fringes; disks large, the first the smallest, all broader than distal digital segments; disk of third finger about ¾ size of tympanum; an oblique tarsal fold continuing along outer margin of first toe to its disk; inner metatarsal tubercle small, elongate; outer tubercle smooth, with a ridge along outer margin; plantar surfaces smooth and with an outer ridge continuing to disk of last toe; subarticular tubercles of toes small, inconspicuous; first toe disk the smallest, followed in size by fifth and second; all disks broader than distal digital segments; toes with an intermediate web; all toes with broad distinct lateral fringes; heel of adpressed hind limb extending anteriorly to middle of eye; a vocal slit on each side, not too close to angle of jaw, and two compact, rugose pouches behind each jaw.

Dorsum smooth except for a few small tubercles at posterior end (under high magnification, dorsum covered with flat, inconspicuous warts); flanks and loreal region smooth; ventral surfaces minutely granular; posterior aspect of thighs smooth.

Color. Dorsum light brown, spotted and mottled with darker brown; an indistinct canthal streak; loreal region, face, and temporal areas light brown, lighter than dorsum; upper flanks approximately the same color as dorsum but with a black band from posterior corner of eye to base of the upper arm; an indistinct, whitish oblique-lateral line from groin to about halfway along flank; hind limb with dark, narrow transverse bars; posterior aspect of thighs same color as dorsum; ventral surfaces immaculate but with some infuscation on throat and chest, especially at base of forelimbs.

Measurements (mm). Snout–vent 21.0; head length 10.0; head breadth 6.8; eye diameter 3.0; eye–nostril 2.0; upper eyelid 2.0; interorbital space 2.3; femur 9.6; tibia 10.3; foot 10.0.

Variation. Specimen MCZ-A 104946 is considered with some misgivings as a paratype, but the presence of the hand pad in both hands of both specimens and the sharing of a very short second finger, much shorter than the fourth, led the author to believe that they belong to the same species although they may eventually be found to be subspecies of each other.

The paratype is a little larger than the type (22.0 mm), slightly less webbed and more distinctly spotted above, but its most distinctive feature is an oblique-lateral stripe that extends from eye to groin. However, the short oblique-lateral stripe of the holotype may have extended to the eye in the living animal and the anterior portion may have faded in preservation. Until more specimens are collected it is not possible to come to a conclusion.

Discussion. Only three members of group VI have been reported from Ecuador and one of the three is still undescribed (Edwards, 1974). This last species is from Río Azuela, in the same river system and relatively close to Reventador, but in this species there is no oblique-lateral stripe, the first finger is said to be longer or equal to the second, the venter is spotted, and there are lateral fringes on the fingers.

The other members of group VI in Ecuador, *C. fuliginosus* and *C. nexipus,* are quite different from *C. maculosus,* and so is a species from western Ecuador, which will be described elsewhere.

Colostethus paradoxus, sp. nov.

Figs. 5a–d

Holotype. MCZ-A 103924, an adult male from Lamtac, Cuenca, 2,535 m, Provincia Azuay, Ecuador. Collector: Giovanni Onore, April 1982.

Etymology. Paradoxus, from the Greek *paradoxos,* strange, contrary to all expectations, in reference to the combination of characters in this species.

Diagnosis. A relatively small *Colostethus* referable to group IV, with dorsolateral and ventrolateral stripes, no oblique-lateral stripe, a dark-colored and well-defined lateral band; a short web between toes II and III, and III and IV, finger disks not broader than the distal digital segments, first finger longer than second, three outer fingers and all toes with a lateral fringe, and male with a dilated third finger.

Description of Holotype. Tip of snout more or less rounded beyond nostrils; rounded when seen from the side; nostrils anterolateral, not protruding; tongue spatulate, entire, not quite ½ free; choanae small, rounded; canthus rostralis rounded but an-

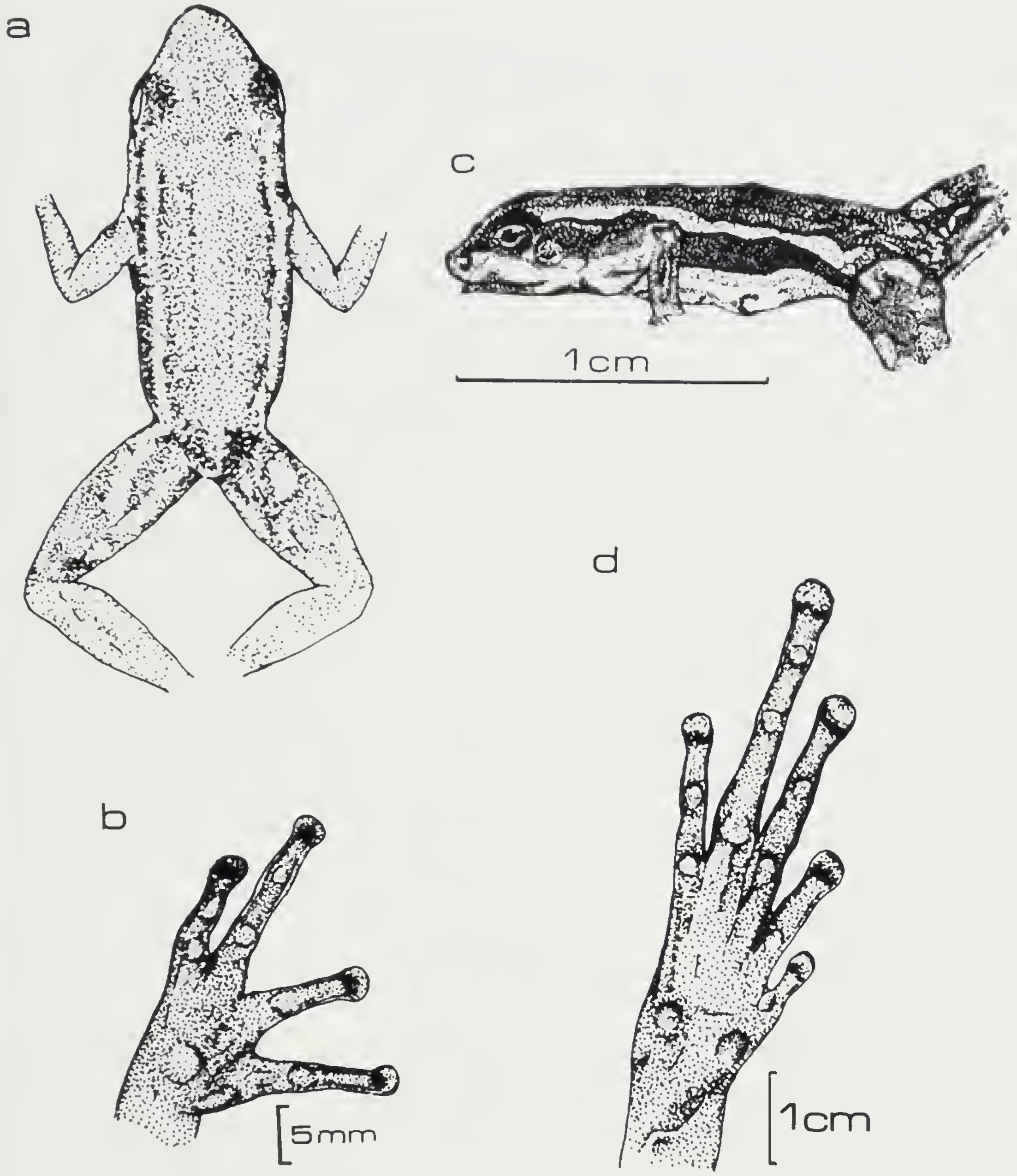

Figure 5. MCZ-A 103924, holotype of *Colostethus paradoxus,* (a) dorsal view; (b) ventral view of hand; (c) lateral view; (d) ventral view of foot.

gular, straight; loreal region vertical, flat; tympanum moderate, its upper half covered by skin; external metacarpal tubercle conical, protuberant; inner tubercle slightly more elongate, less protuberant; palm of hand smooth, with a ridge along outer margin; subarticular tubercles large, proximal of first finger and distal of fourth, smaller than others; first finger longer than second, second slightly shorter than last; third finger dilated; three outer fingers with distinct lateral fringes; disks not broader than distal digital segments and all more or less of same size; disk of third finger not more than ⅓ size of tympanum; a transverse, short, tarsal fold; metatarsal tubercles conical, prominent, with inner tubercle slightly more elongate than outer tubercle; plantar surfaces smooth, with a slight ridge along outer edge that continues to disk of fifth toe; a minimal web between toes II and III, and III and IV; except for first disk, all others slightly broader than distal digital segments; toes with lateral fringes; heel of adpressed hind limb extending anteriorly to between eye and nostril; a pair of vocal slits not too close to angle of jaw.

Dorsum smooth except for a few tubercles between insertion of hind limbs, and a fringe of tubercles margining fold above cloaca; loreal region and flanks smooth; ventral surfaces, including posterior aspect of thighs, smooth; posterior aspect of upper arm smooth.

Color. Above, solid light brown; two lighter colored dorsolateral stripes from posterior corner of eye crossing to groin and extending for short distance on thighs; black lines along the anterior or posterior aspects of forearms or thighs absent; loreal and temporal regions, including lower edge of tympanum, cream, this light color extending posteriorly as a ventrolateral stripe; a short brown streak below eye; thigh with a brownish bar between whitish area of proximal portion and with another one closer to knee; two elongate, whitish spots on posterodorsal aspect of thighs; forelimbs and rest of hind limbs uniform light brown; a canthal streak; flanks with a distinct and well-defined dark brown band from behind eye to groin; white ventrolateral stripe margined below by an irregularly margined brown streak; ventral surfaces infuscated and marbled on throat and limbs, but much less so on belly (except for the brown lateral streaks described above); whitish or unpigmented areas present in feet, metatarsal segments, and tibial segments.

Measurements (mm). Snout–vent 19.5; head length 6.2; head breadth 6.0; eye diameter 2.7; eye–nostril 2.0; eye–tip of snout 3.0; upper eyelid 3.4; interorbital space 3.1; femur 7.8; tibia 9.9; foot 8.2.

Discussion. The swollen third finger of the male places *Colostethus paradoxus* in group IV. However, this species is very similar to some members of group II, particularly *C. kingsburyi* and a species from Cochabamba, Bolivia, reported by Edwards (1974). It also has the dorsolateral and ventrolateral stripes and the distinct and continuous dark lateral band that characterize members of group II, but in this respect, it is not different from *C. pratti,* which also has a dilated third finger and is a clear member of group IV. *C. talamancae* on the other hand, has dorsolateral and ventrolateral stripes and a dark lateral band but the males do not have a dilated third finger, which is the reason why Rivero (1988) suggested that it could be a member of group II in spite of its distribution, west of the Andes. This only serves to confirm the close relationship between groups II and IV, but whether a dilated third finger has arisen independently in different members of group II cannot be confirmed at present.

Rivero and Serna (1988) indicated that group IV was typical of western Colombia (and Central America) and that it did not extend southwards beyond Quevedo in northern Ecuador. Yet, *C. paradoxus* is from Southern Ecuador and it doesn't show any relationship to the only Ecuadorian member of group IV (still undescribed; Edwards, 1974). In spite of its dilated third finger it seems to be closer to the East Andean members of group II. If it is to be related to any member of group IV, it is to *C. pratti* and perhaps *C. latinasus,* but these are only found in Central America and in Colombia, west of the Oriental Cordillera.

Colostethus faciopunctulatus, sp. nov.
Figs. 6a–c

Holotype. MCZ-A 94751, an adult male from Puerto Nariño (3°46′N, 71°23′W, 15 km W. of Leticia), Departamento Amazonas, Colombia. Collector: R. Bleiweiss, 19 July 1977.

Paratypes. MCZ-A 94746–50, 94552–6, 93782, 94757–61, 96016–7, all from the same locality and collected by R. Bleiweiss, but 93782 collected on July 9, 94757–60 on July 19–21, 96016–7 on July 27, and 94761 on July 31.

Etymology. Faciopunctulatus, from the Latin *facies,* face, and *punctulatus,* dotted, in reference to the white dots on the loreal region, under the eye, and in the temporal region of this species.

Diagnosis. A medium-size *Colostethus* referable to group VI, with extensive webbing between the toes, generally with contrast-

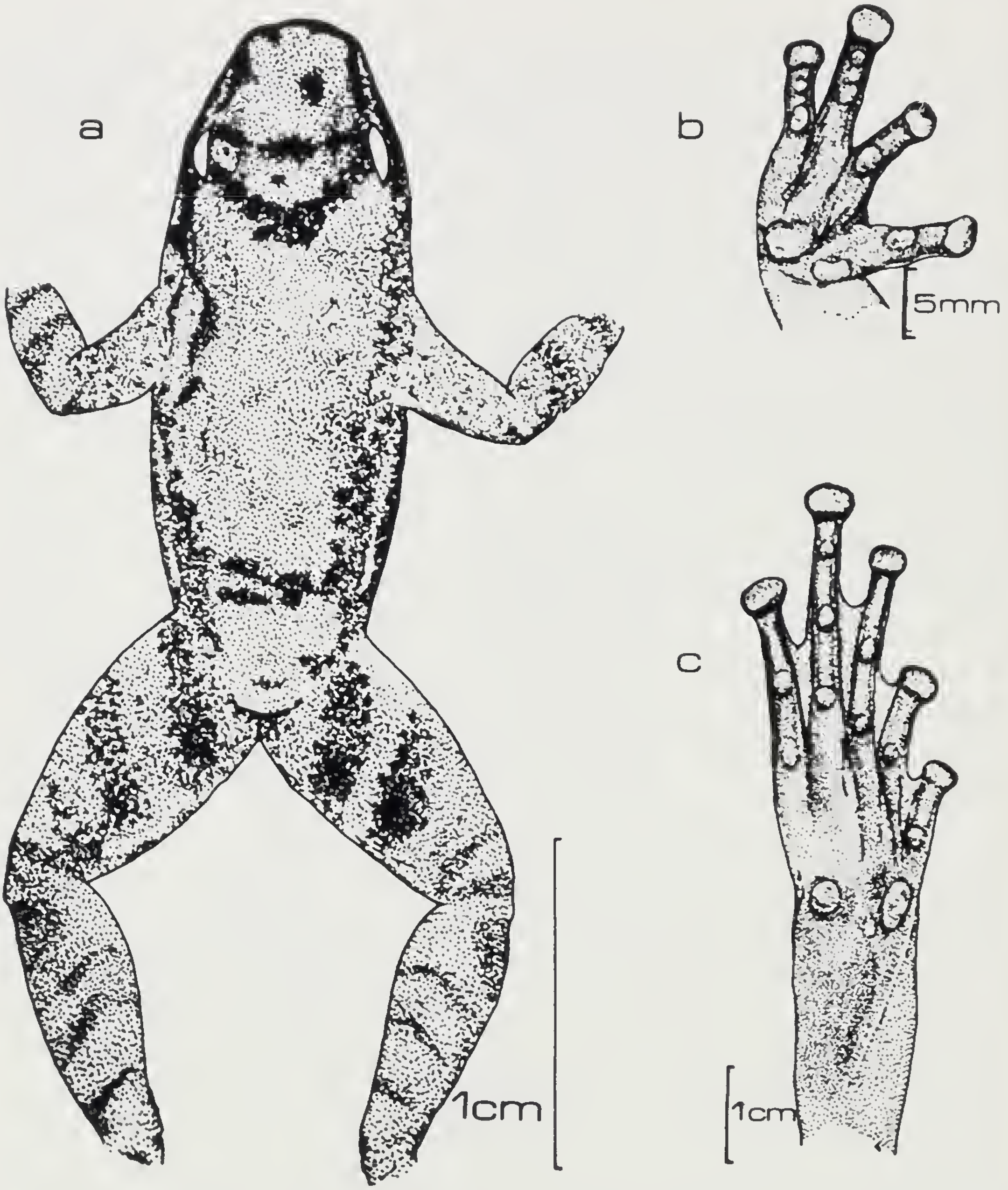

Figure 6. MCZ-A 94751, holotype of *Colostethus faciopunctulatus,* (a) dorsal view; (b) ventral view of hand; (c) ventral view of foot.

ing white dots on the loreal area, under the eyes, and in the temporal region, distinct ventral sexual dichromatism, the males having a blackened throat with white dots, short fingers, the second considerably reduced, no dorsolateral, ventrolateral, or oblique-lateral stripes, and a gray dorsum, usually with contrasting, black, V-shaped or transverse markings in back of the eyes and behind the sacral hump.

Description of Holotype. Tip of snout truncate, almost vertical when seen from side; nostrils lateral, slightly protuberant; tongue spatulate, indented behind, and about ⅔ free; choanae small, ovate; canthus rostralis somewhat rounded, curved; loreal region slightly slanting and concave; tympanum moderate, not particularly distinct, covered posterolaterally by skin; external metacarpal tubercle rounded; inner tubercle narrow, elongate; palm of hand smooth, with no apparent ridge or fold on outer edge; subarticular tubercles moderate, not too prominent; fingers short; first finger slightly longer than second, second shorter than last; fingers without lateral fringes; disks moderate, of approximately equal size, broader than distal digital segments; disk of third finger a little more than ⅔ size of tympanum; a short, oblique tarsal fold extending as a fringe along outer margin of first toe; metatarsal tubercles prominent, with outer tubercle rounded and inner tubercle elongate; plantar surfaces smooth, with a ridge along outer edge; pedal web intermediate; disks of toes broader than distal segments; first and last toe disks smaller than others; a distinct lateral fringe on toes; heel of adpressed hind limb extending anteriorly to middle of eye; a pair of vocal slits close to angle of jaw.

Dorsal surfaces smooth; loreal region and flanks smooth; abdomen and throat granular.

Color. Above, gray with a black, contrasting bar between the eyes, another V-shaped bar in back of the eyes, and a few smaller spots in back of the sacrum; a canthal streak; a short black bar between eye and base of arm; loreal region, area under eye, and temporal region blackish, with contrasting white dots; flanks a little darker than dorsum and with one or two white spots near inguinal region; a white or very little pigmented area in axilla; thighs and tibiae with indistinct dark blotches; posterior aspect of thighs indistinctly marbled black and tan; throat blackish (this color more intense on sides) and with white dots; abdomen white, with milky white dots on posterior end; arm tubercles white; ventral aspect of arms and posterior proximal aspect of thighs dark gray with white dots; no dorsolateral, ventrolateral, or oblique-lateral stripes; longitudinal black lines on the anterior and posterior aspects of arms or thighs absent.

Variation. There is a distinct ventral sexual dichromatism, the males having a blackened throat with white dots while the females are uniformly colored. The white dots on the side of the head and the ventral portion of the thighs and forelimbs are either absent or inconspicuous in the females.

The first finger is slightly longer than the second in two male specimens (including the type), shorter than the second in both females and one adult male, and equal to the second in one male. The first finger is shorter than the second in two juveniles and longer in one.

The dots on the side of the head are present, in various degrees of distinctness, in all individuals except in one female, but the dots on the flanks are absent in four juveniles, and those on the lower aspect of the thighs are absent in most.

The dorsal color may be light gray or brownish gray, with contrasting dorsal markings, or very dark gray with imperceptible markings. The discolored area of the axillae is present in all specimens but may not be noticeable in those in which it is continuous with the ventral coloration.

Juveniles tend to be of a tan or light yellowish brown color with contrasting dorsal spots and better-defined bars on the legs. The white ventral dots are present in most individuals, and certainly on the throat of all males, but the abdominal dots may only be evident under a lens.

Granules are present on the abdomen but not evenly distributed in most cases and absent in some cases.

Measurements and Proportions. See Table 3.

Discussion. Colostethus faciopunctulatus is a clear member of group VI (as restricted), although in all members of that group the first finger is almost always shorter than the second, while in a few specimens of *C. faciopunctulatus* the first finger is slightly longer and in others it is equal to the second.

Distinctive features of *C. faciopunctulatus* are the white dots on the face, the very reduced second finger, and the usually contrasting dark bars or splashes on the dorsum.

The only member of group VI reported from eastern Colombia is *C. fuliginosus,* and the only members from eastern Ecuador are, besides *C. fuliginosus, C. nexipus* and an undescribed species from Río Azuela (between Quito and Lago Agrio), 1,740 m, Napo, Ecuador (Edwards, 1974).

Table 3. *Colostethus faciopunctulatus* measurements and proportions.

Catalog	Males					Females			
No.	94751	94749	93782	94746	Average	94761	94750	94752	Average
SV	21.40	23.70	22.80	21.20	22.28	23.50	25.25	22.75	23.83
HB	7.70	8.60	7.50	7.60	7.85	9.25	9.10	8.55	8.97
HL	8.00	9.20	8.20	7.00	8.10	9.00	9.30	8.50	8.93
ETS	3.00	4.20	3.80	3.90	3.73	4.10	4.20	3.50	3.93
EN	2.70	2.25	2.00	2.30	2.31	2.65	2.40	2.30	2.45
IOS	2.80	2.45	2.80	2.20	2.56	2.50	2.90	2.25	2.55
UE	2.20	2.15	2.60	2.20	2.29	2.40	2.55	2.10	2.35
ED	3.20	3.55	3.00	3.80	3.39	3.50	3.65	3.30	3.48
DT	1.50	1.40	2.10	1.20	1.55	1.45	1.60	1.65	1.57
LF	10.00	11.00	11.50	10.01	10.63	11.70	11.60	11.40	11.57
LT	10.10	11.10	10.15	10.70	10.51	11.40	10.60	10.60	10.87
LFT	8.90	9.95	10.50	8.70	9.51	10.65	9.60	9.00	9.75
HB/SV	0.36	0.36	0.33	0.36	0.35	0.39	0.36	0.38	0.38
HL/SV	0.37	0.39	0.36	0.33	0.36	0.38	0.37	0.37	0.37
UE/IOS	0.79	0.88	0.93	1.00	0.90	0.96	0.88	0.93	0.92
DT/ED	0.47	0.39	0.70	0.32	0.47	0.41	0.44	0.50	0.45
ED/ETS	1.07	0.85	0.79	0.97	0.92	0.85	0.87	0.94	0.89
ED/EN	1.19	1.58	1.50	1.65	1.48	1.32	1.52	1.43	1.43
LF/SV	0.47	0.46	0.50	0.47	0.48	0.50	0.46	0.50	0.49
LT/SV	0.47	0.47	0.45	0.50	0.47	0.49	0.42	0.47	0.46
LFT/SV	0.42	0.42	0.46	0.41	0.43	0.45	0.38	0.40	0.41
LF/LT	0.99	0.99	1.13	0.94	1.01	1.03	1.09	1.08	1.07

For key to characters see Table 1a.

The Río Azuela species also has white specks on the upper lip, but the dorsum is chestnut brown with faint white spots, adult females grow to 28–31 mm, and the color of the belly is light with darker spots.

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ON SOME OVERLOOKED SPECIES OF THE GENUS *LIOLAEMUS* WIEGMANN (REPTILIA TROPIDURIDAE) FROM PERU

R. F. LAURENT[1]

ABSTRACT. Three new species of the genus *Liolaemus, L. robustus, L. polystictus,* and *L. williamsi,* from the upper western slopes of the Cordillera Central and of the eastern slopes of the Cordillera Occidental of Peru are described. They were previously confused with *L. multiformis* Cope, 1856, which is here synonymized with *L. signifer* (Duméril and Bibron, 1841) and seems to be restricted to the northern part of the Altiplano. The status of other northern species of *Liolaemus* is discussed.

INTRODUCTION

The bewildering diversity of the genus *Liolaemus* Wiegmann has been well documented by L. Müller, W. Hellmich, R. Donoso-Barros, and J. M. Cei for the southern part of its range in Chile and Argentina, more or less south of the 30th parallel. In contrast, this diversity has been largely neglected in the northern part of its range, in northwestern Argentina, Bolivia, and Peru. Many of the forms that occur in this region have been inadequately described, and a number of names have been placed in synonymy with little or no documentation. Thus, the discovery of three undescribed species from the upper western slopes of the Cor-

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Table 1. Characters of the subgenera *Liolaemus* and *Eulaemus*.

	Liolaemus (395 ♂♂, 356 ♀♀)	*Eulaemus* (313 ♂♂, 313 ♀♀)
Preanal pores	0–7 $\bar{x} = 2.19$ <5 in 91% of specimens, the series generally shorter than the 1st toe (12.4% of exceptions)	3–12 $\bar{x} = 6.40$ >4 in 92% of specimens, the series generally longer than the 1st toe (2.29% of exceptions)
Nostrils	lateral	latero-dorsal
Distance between upper border of subocular and lip compared with distance between nasal plates	inferior (3.37% of exceptions)	superior (7.03% of exceptions)
Upper labials	generally flat and long, the 4th below eye, with posterior border oblique	generally high and short, 5th, 6th, or 7th below eye, with posterior border vertical
Range	Chile (≥50 taxa) southern and western Argentina (18 taxa) Bolivia (3 taxa) Peru (3 taxa)	northern Chile (6 taxa) southern and western Argentina (25 taxa) Bolivia (6 taxa) Peru (9 taxa)

dillera Central and the upper eastern slopes of the Cordillera Occidental of Peru necessitates an evaluation of the status of other taxa from the region, before the new forms can be adequately diagnosed.

Elsewhere (Laurent, 1983), I have pointed out that the great majority of *Liolaemus* species, including all that occur in the northern part of its range, can be referred to one or the other of two large groups: 1) a primarily Chilean group (subgenus *Liolaemus*), and 2) a primarily Argentinian group (subgenus *Eulaemus*). Distinguishing characteristics of these two groups are provided in Table 1.

Two groups of *Eulaemus* may be recognized: 1) a *fitzingeri* group in which there is a patch of enlarged scales on the posterior surface of the thigh, and 2) a *signifer* group in which the patch of enlarged scales is lacking. The species allocated to the subgenus

Liolaemus and to the two subgroups of *Eulaemus* are listed in the Appendix.

Members of the Chilean group (subgenus *Liolaemus*) are few in the northern part of the range of *Liolaemus*. *Liolaemus tacnae* (Shreve), originally described in the genus *Stenocercus,* is apparently a local species from the department of Tacna in southern Peru. *Liolaemus alticolor* Barbour and *L. walkeri* Shreve are names that have been applied to a large set of Andean populations from Peru southward to Catamarca Province, Argentina. The form *walkeri* was considered by Hellmich (1961) and Donoso-Barros (1966) to be a subspecies of *alticolor*. It is uncertain whether this form represents a valid species or subspecies. In fact, several taxa may be represented by specimens now referred to *walkeri*.

The majority of northern *Liolaemus,* including the three new species described below, are members of the Argentinian group (subgenus *Eulaemus*). A number of Koslowsky's names have been revived (Laurent, 1982a) for members of this group, and new species have been recently described (Laurent, 1982a, 1984, 1985, 1986), but there still are problems with certain other names in the group.

Liolaemus ornatus Koslowsky, 1898, is an abundant species of the *fitzingeri* group that occurs from low to high altitudes from Catamarca Province, western Argentina, northward to the Lake Titicaca region in southern Peru and northern Bolivia. Pellegrin (1909) described *Liolaemus pulcher* and *L. mocquardi* from Tiahuanaco, Depto. de La Paz, Bolivia. Examination of the syntypes reveals that those of *L. pulcher* are males and those of *L. mocquardi* are females of the same form. Peters and Donoso-Barros (1970) correctly placed *L. pulcher* in the synonymy of *L. ornatus,* thus *L. mocquardi* may now be added to that synonymy.

Liolaemus simonsi Boulenger, 1902, based on specimens from Potosi, Challapata, and Uyuni, Bolivia, was considered to be a subspecies of *multiformis* by Burt and Burt (1931), an allocation followed by Peters and Donoso-Barros (1970). The syntypes of *Liolaemus simonsi* (BM 1902.5.29.74–79 [RR 1946.8.12.20–23], 1902.5.29.85–87 [RR 1946.8.12.24–26]), kindly lent by Dr. C. MacCarthy, possess a patch of enlarged scales on the posterior aspect of the thigh, a fact not mentioned in the type description, but which excludes *simonsii* from the synonymy of *multiformis.*

However, a comparison of the syntypes with Bolivian specimens of the widespread *Liolaemus ornatus* confirm the synonymy of *simonsi* with *ornatus*.

The remaining northern species of *Liolaemus*, including the three new forms described below, are members of the *signifer* group of *Eulaemus*. *Liolaemus dorbignyi* Koslowsky, 1898, from Catamarca Province in western Argentina and *L. jamesi* Boulenger, 1891, from west of the Andes in Tarapacá Province, northern Chile, are large-scaled members of the *signifer* group, similar to one another in scalation and proportions, and may represent vicariant forms on opposite sides of the Andes, an hypothesis to be investigated in a later paper.

Liolaemus signifer (Duméril and Bibron, 1841) is one of the two oldest names available for members of the Argentinian group, the other is *L. fitzingerii*. The type locality of *L. signifer* was given as "Chile," but recently Cei, Lescure, and Ortiz (1980) have mapped the route taken by d'Orbigny, its collector, in Chile, Peru, and Bolivia, and restricted the type locality of *signifer* to the highlands of Peru and Bolivia. For the most part, the route taken by d'Orbigny passed through the range of the species that most subsequent authors refer to as *Liolaemus multiformis* Cope with a very short stretch passing through the range of *Liolaemus annectens* Boulenger, 1901, in Arequipa Province, Peru. There are significant statistical differences between these two forms, but the presence of a zone of intergradation indicates that a single species with two geographic races is involved. When the holotype of *L. signifer* (MNH Paris 6890) is compared with the two races, it falls always with the population of the intergrade zone or with *multiformis,* never with *annectens*. It is on this basis that *Liolaemus multiformis* Cope, 1856, is here considered to be a synonym of *L. signifer* (Duméril and Bibron, 1841).

L. multiformis was based on a series of specimens (Acad. Nat. Sci. Phila. 13064–6, 13098, 13104, 13168–70) from Lake Titicaca, Peru. A number of forms described subsequently have been placed in its synonymy, some correctly, but some apparently not. I have examined all of the relevant type material and consider the following synonymies to be correct: *lenzi* Boettger, 1891 (fide Burt and Burt, 1931), type locality "Bolivianische Ufer des Titicaca-Sees"; *tropidonotus* Boulenger, 1901 (fide Burt and Burt,

1931), type locality "Tirapata, E. Peru, 13,000 feet"; *bolivianus* Pellegrin, 1909 (fide Hellmich, 1962), type locality "Tiahuanaco, Depto. de La Paz, Bolivia"; *variabilis crequii* Pellegrin, 1909 (fide Hellmich, 1962), type locality "Tiahuanaco, Depto. de La Paz, Bolivia"; *variabilis courtyi* Pellegrin, 1909 (fide Hellmich, 1962), type locality "Tiahuanaco, Depto. de La Paz, Bolivia"; *variabilis neveui* Pellegrin, 1909 (fide Hellmich, 1962), type locality "Tiahuanaco, Depto. de La Paz, Bolivia."

Since *multiformis* has been shown to be a synonym of *signifer,* all of the above forms are properly referred to the synonymy of the latter. In addition, *L. pantherinus* Pellegrin, 1909 (syntypes MNH Paris 05-344–05-345), for which no locality was given, also cannot be distinguished from *L. signifer.*

Two forms that have been synonymized with *Liolaemus multiformis* appear to be valid: *L. annectens* Boulenger, 1901 (synonymized by Hellmich, 1962), type locality "Caylloma and Sumbay, 11,300 to 13,600 feet," and *L. annectens orientalis* Müller, 1923 (synonymized with *multiformis simonsi* Boulenger, 1902, by Burt and Burt, 1931), type locality "Oberer Pilcomayo, zwischen Tarija and S. Francisco, Bolivien." As pointed out above, *Liolaemus annectens* is probably a geographic race of *Liolaemus signifer.* Evidence for the validity of *orientalis* will be presented at another time.

As indicated earlier, the *signifer* group of *Eulaemus* is defined by the absence of a patch of enlarged postfemoral scales, while the *fitzingerii* group is defined by their presence. A patch of enlarged postfemoral scales is unique within tropidurine iguanids and is almost certainly derived. However, if a patch of enlarged postfemoral scales was derived only once within *Liolaemus,* then the *fitzingerii* group is paraphyletic, because the patch is also found in species excluded from the group and placed in the subgenus *Ortholaemus* (Laurent, 1984), i.e., *wiegmanni, cranwelli, multimaculatus, scapularis, salinicola, occipitalis, lutzae.* Since the *signifer* group, at present, is defined only by the absence of these enlarged scales, this subgroup also may be paraphyletic. Although the question of their monophyly cannot be resolved at this time, the *signifer* and *fitzingerii* groups provide a useful means for the diagnoses and identification of the new forms described below.

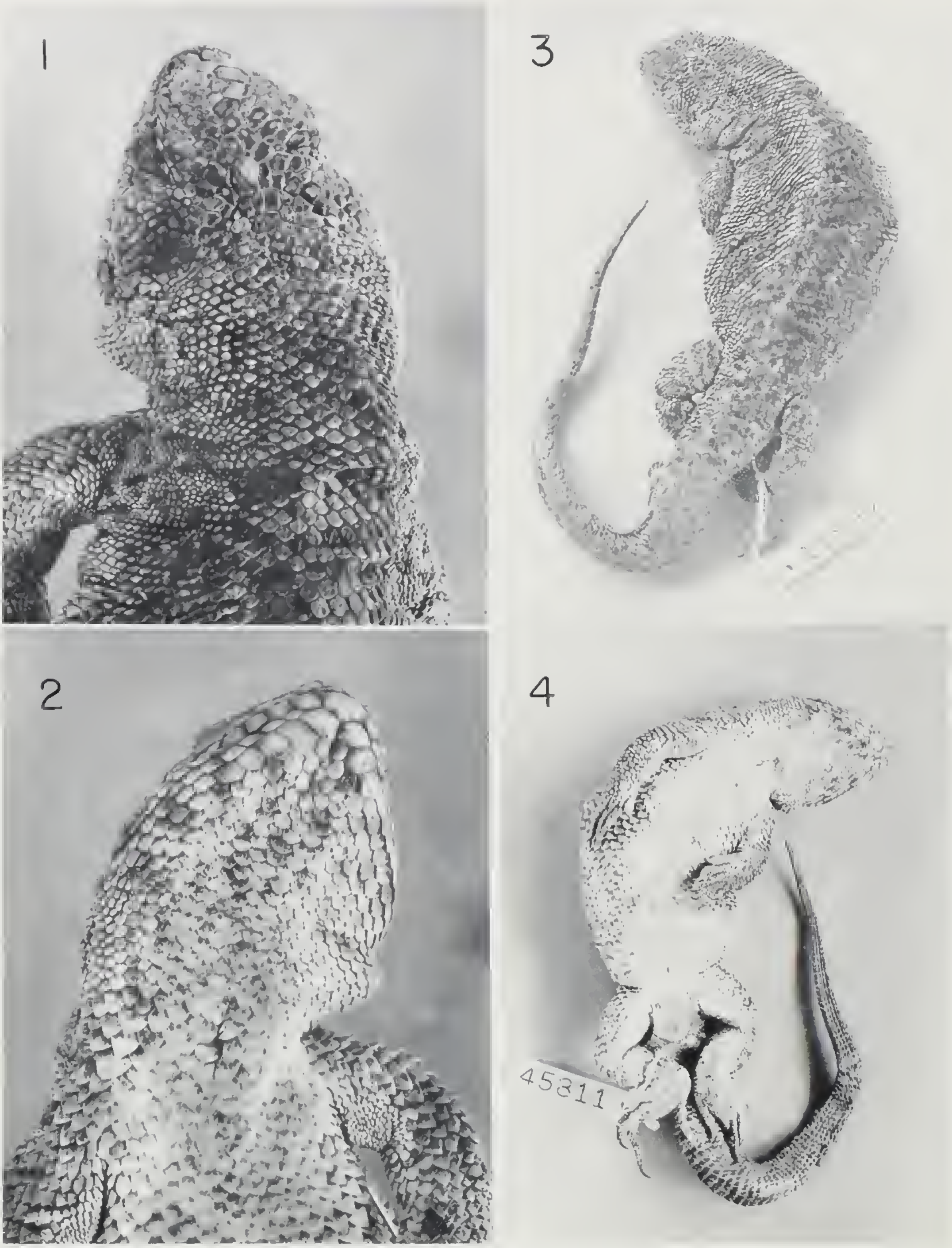

Plate I. *Liolaemus robustus,* sp. nov. Paratype male: MCZ 45811. Depto. Junin, Peru. 1. Dorsal view of head. 2. Ventral view of head. 3. Dorsal view. 4. Ventral view.

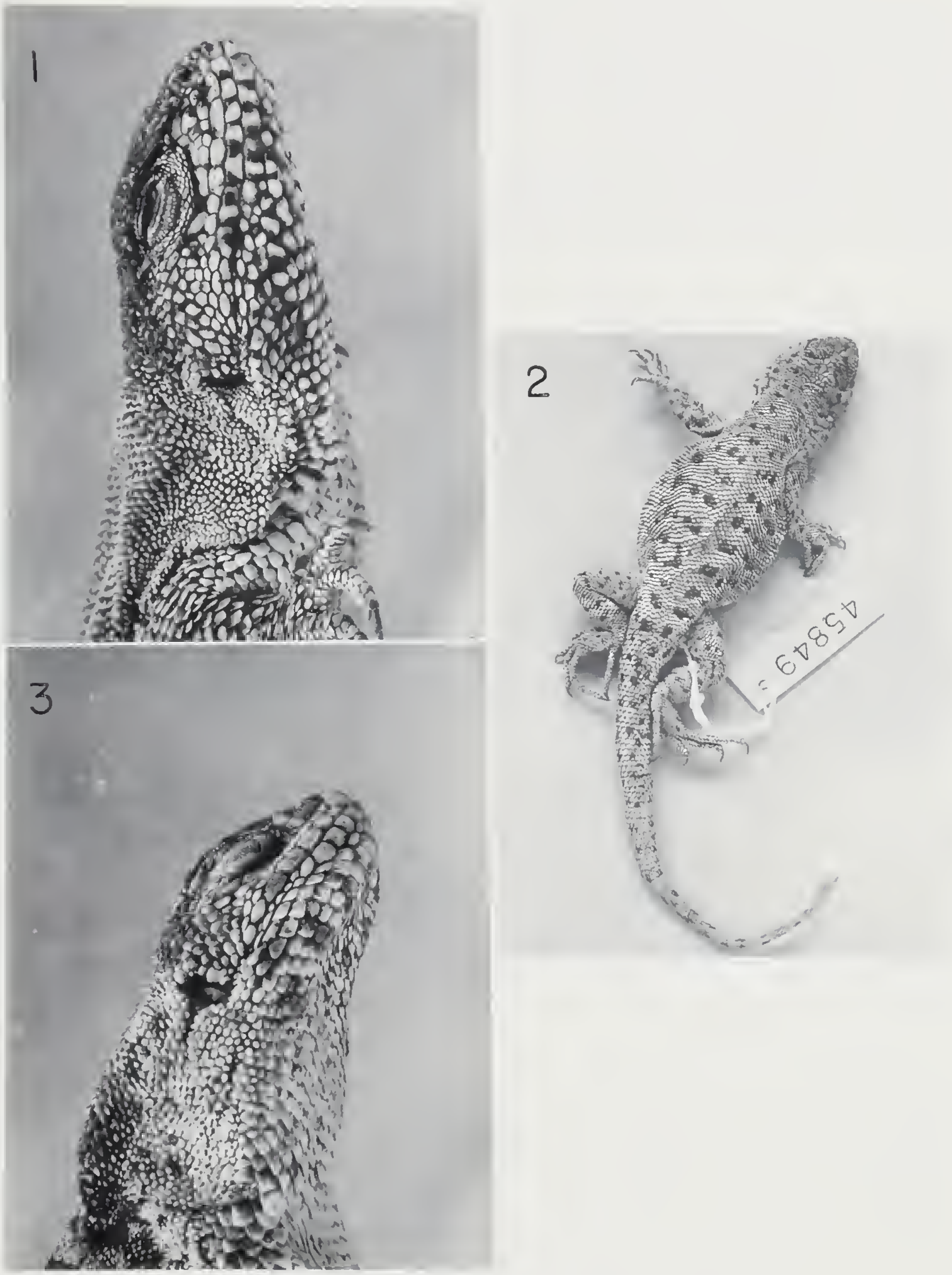

Plate II. 1. *Liolaemus polystictus,* sp. nov. Holotype male: MCZ 45845. Side view of head. 2. *Liolaemus polystictus,* sp. nov. Paratype female: MCZ 45849. Dorsal view. 3. *Liolaemus robustus,* sp. nov. Paratype female: MCZ 45811. Side view of head.

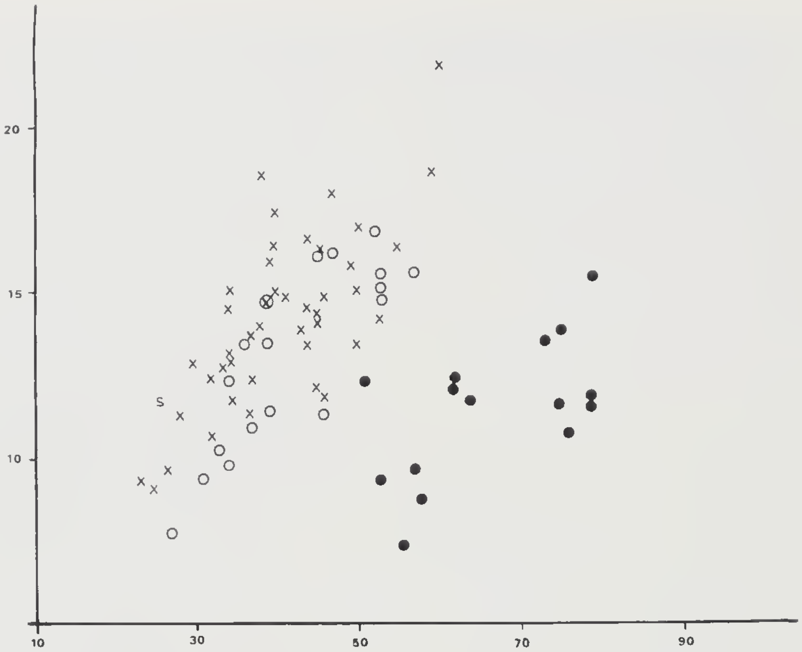

Figure 1. Scatter-diagram of minimum width of frontal region (ordinates) and length of 5 dorsal scales (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus signifer,* ○ = *L. polystictus,* sp. nov. ● = *L. robustus,* sp. nov. S = Type of *L. signifer.* ⊗ = Lectotype of *L. multiformis.*

Liolaemus robustus, new species
(Pl. I, Figs. 1–4; Pl. II, Fig. 3)

Holotype. One male (FMNH 34242/H) from Junin, Depto. Junin, collected by K. P. Schmidt.

Paratypes. PERU: *Depto. Junin:* Same data as holotype: FMNH 34242/1–23, 34247, 11 males, 4 females, 9 juveniles. Huayre, N of Junin: FMNH 34253, 2 males, 1 female, 4 juveniles. Huawhay (=Huayre ?): UMMZ 89484, 1 male. Ondores on Lake Junin: MCZ 157226, 1 male. "Dept. of Junin" only: MCZ 45809–12, 16155–56, 1 male, 5 females, W. F. Walker, 14 April 1939. *Depto. Lima:* Yauricocha: MCZ 45830, 1 male.

Diagnosis. A species of the *Liolaemus signifer* group, differing from *L. signifer* by the lower number of scales around the body (47–61, instead of 66–82), the frontal azygous, generally divided in two parts, anterior and posterior, instead of divided into many scales (at least 3, generally 5–8, and even more), by a narrower frontal zone, bigger head, more robust general proportions, and by its characteristic color pattern with black spots or dots.

Other differences are: 1) 44–59 scales (rather than 65–87) between occiput and level of the front border of the thighs; 2) 12–19 dorsal scales (instead of 18–30) in head length; 3) 63–78 ventral scales (instead of 74–92) between postmentals and vent; 4) 49–70 lateral scales between the legs (instead of 65–89); 5) minimum width of frontal region 13–25% (rather than 25–49%) of the length of 5 dorsal scales (see Fig. 1).

Description of the Holotype. Head length (from posterior edge of ear opening) (HL = 20.13 mm) 26.8% of snout–vent length (SVL = 77 mm). Two vertical antehumeral folds and a longitudinal oblique and sinuous fold on the side of the neck, bifurcated behind the ear on the right side. Scales on the upper side of head markedly convex, a count of 15 on the midline. Rostral scale about 2.5 times as wide (W = 4.0 mm) as high (H = 1.63 mm). Nasal triangular, separated from rostral, surrounded by 7 scales. Nostril round, in the posterior part of the nasal, a little nearer to the point of the snout (2.94 mm) than to the posterior extremity of the canthal (3.40 mm). Internasals 2 anterior + 2 azygous + 2 posterior. Ear opening somewhat oblique, nearly rectangular, surrounded by granular scales that are smaller behind than in front of the ear. Temporals convex, 7 between the postsubocular and the ear. Interparietal small, pentagonal, surrounded by 5 scales, the anteriormost median. Frontal region occupied by 2 azygous scales. Five supraoculars, 7 supraciliaries, the 5th below the 4th and 6th. Five scales between the rostral and frontal region. Semicircles simple, 4 scales between the frontal region and the supraciliaries.

In prefrontal zone, between the posterior internasals and the frontal region, 11 scales, 3 intercanthal scales. Across the snout, 11 scales between the labials at the postnasal level, 11 also at the canthal level. Four scales between nasal and subocular. Subocular divided in two. Paralabials 8, 4 in contact with subocular. Supralabials 8. Infralabials 5–6, followed by 9–7 granules as far as the corner of the mouth. Mental fan-shaped, in contact with 4 scales.

Lateral scales of neck granular, 41 between ear opening and forelimb. About 30 scales between ear openings. Fifty-five scales around the body. Fifty-four between occiput and level of anterior border of thigh. Dorsal scales juxtaposed or imbricate on the sides, very faintly keeled or smooth, 14 in head length. Flank scales smaller, erect, granular at armpit and groin, about 61 between legs. Ventrals smooth and imbricate, 68 between mental and preanal pores. Caudal scales similar to body scales, 22 in 15th verticil. No patch of enlarged scales behind the thigh. Fourteen to fifteen infradigital lamellae beneath 4th finger, 19 beneath 4th toe. Tail (83 mm) 107.8% of snout–vent length.

Color (in Alcohol). Above, olivaceous gray, with some scales blackish, these often clustered in small groups, which give a more or less punctate appearance. Belly whitish with grayish pigmentation on most scales; throat with gray dots, without definite pattern.

Variation (see Table 2). Upper labials generally 8 (38 sides), sometimes 9 (16 sides) or 7 (9 sides), rarely 10 (5 sides) or 11 (2 sides), the first 5 to 6 without small scales below and inside. Lower labials generally 6 (46 sides), sometimes 5 (14 sides), rarely 7 (6 sides), 8 (3 sides), or 4 (1 side). Supraoculars generally 4 (34 sides) or 5 (25 sides), rarely 6 (7 sides) or 3 (8 sides). Supraciliaries usually 7, the 5th below the 4th and 6th, but 6 on 6 sides and 8 on 9 sides. Temporals between the postsubocular and the ear most often 8 (31 sides), not infrequently 7 (24 sides), sometimes 9 (11 sides), exceptionally 6 (4 sides). Plates between the rostral and the frontal normally 5 (43 sides), sometimes 6 (20 sides), rarely 7 (3 sides) or 4 (2 sides). Scales between the frontal and the supraciliaries 4 (46 sides), sometimes 3 (19 sides), rarely 2 (3 sides) or 5 (2 sides). Scales around the interparietal usually 5 (11 cases) or 6 (14 cases), sometimes 7 (7 cases), rarely 8 (3 cases), symmetrical (14 cases) or irregular (21 cases). Scales in contact with the nasal generally 7 (35 sides), sometimes 6 (19 sides) or 8 (11 sides), rarely 9 (2 sides) or 5 (1 side), rarely adjacent to the rostral (2 sides). Paralabials usually 8 (28 sides), often 7 (22 sides), sometimes 9 (13 sides), rarely 6 (4 sides) or 10 (1 side). Paralabials in contact with subocular generally 4 (41 sides), sometimes 5 (18 sides), rarely 3 (7 sides), exceptionally 2 or 6 (1 side each). Plates between the upper labials over the snout posterior to the nasals 7 to 12 (mean = 9.97), at canthal level 9 to 14 (mean = 11.60). Usually 4 scales between nasal and subocular. Preanal pores in males 3 (2 cases), 4 (8 cases), 5 (6 cases), or 6 (3 cases). A single female has one vestigial pore. Almost always, the frontal is di-

TABLE 2. MERISTIC CHARACTERS OF *LIOLAEMUS ROBUSTUS*.

	(7 ♂♂, 7 ♀♀)	
	♂♂	♀♀
Scales around midbody	48–61 ($\bar{x}$ = 53.05)	50–60 ($\bar{x}$ = 54.43)
Dorsal scales between occiput and levels of anterior border of thighs	44–59 ($\bar{x}$ = 52.28)	51–56 ($\bar{x}$ = 53.14)
Ventral scales between postmentals and vent	63–74 ($\bar{x}$ = 68.59)	72–78 ($\bar{x}$ = 74.14)
Lateral scales between anterior and posterior limbs	49–68 ($\bar{x}$ = 58.40)	56–68 ($\bar{x}$ = 62.14)
Scales in the 15th verticil of tail	18–22 ($\bar{x}$ = 20.28)	19–23 ($\bar{x}$ = 20.86)
Gular scales between ears	29–35 ($\bar{x}$ = 32.04)	28–32 ($\bar{x}$ = 30)
Hellmich's index	14–17 ($\bar{x}$ = 15.40)	13–15 ($\bar{x}$ = 14)
Lamellae under 4th finger	14–17 ($\bar{x}$ = 15.63)	14–16 ($\bar{x}$ = 15)
Lamellae under 4th toe	18–21 ($\bar{x}$ = 19.78)	19–21 ($\bar{x}$ = 19.57)

vided into two plates, one anterior and one posterior. In only three cases are there 3 plates with 2 anterior, one posterior. In one case there are 3 plates in a longitudinal series, in another the anterior plate is asymmetrically located on the left. In three specimens there is a single undivided frontal.

The dorsal coloration does not appear very variable in preserved material. The black dots or spots may be more or less distinct. They have a tendency to concentrate in two laterodorsal zones in some specimens. The ventral pigmentation may be almost absent, uniformly distributed or scattered into ill-defined spots. Intact tails vary from 106 to 123% of snout–vent length in males (mean = 111.47), from 109 to 126% (mean = 117.73) in females.

Size. Snout–vent length of the largest male (from Yauricocha) 85 mm, of the largest female 82 mm.

Geographic Variation. One specimen (MCZ 45830) from Yauricocha, Lima Department, is somewhat different from the other specimens from Junin Department. The belly and throat are black with white dots; the frontal is divided in three; there are 5 scales between the frontal and the supraciliaries, 22 lamellae beneath the 4th toe. The supraciliaries are only 5, the 3rd below the 2nd and 4th. The last may be an anomaly, since the formula 7 (5) is

Table 3. Comparative variation of meristic and morphometric characters in *Liolaemus robustus*, sp. nov., *L. polystictus*, sp. nov., *L. williamsi*, sp. nov., and *L. signifer* (Duméril and Bibron).

	robustus (N = 15)	*polystictus* (N = 17)	*williamsi* (N = 15)	*signifer* (=*multiformis*) (N = 32)
Frontal divided into plates	2 (1 + 1), rarely 3 (2 + 1)	1 to 5 (2 + 1 + 2)	1 to 5 (2 + 1 + 2 or 2 + 2 + 1)	3 (1 + 2) to 9 (3 + 2 + 2 + 2)
Scales around midbody	48–61	57–70	54–67	66–82
Dorsal scales between occiput and level of front borders of thighs	44–59	55–70	48–65	65–87
Ventral scales between postmentals and vent	63–78	62–71	67–78	74–92
Lateral scales between legs	49–68	54–76	66–77	65–89
Hellmich's index	12–17	14–21	17–22	18–30
Minimum width of frontal region as % of length of 5 dorsal scales	13–23 ($\bar{x}$ = 16.9)	24–38 ($\bar{x}$ = 31)	18–29 ($\bar{x}$ = 23.8)	25–49 ($\bar{x}$ = 35.72)
Width of head in % of snout–vent length	19.6–24.6 ($\bar{x}$ = 21.68)	19.70–23.7 ($\bar{x}$ = 21.25)		18.3–22.3 ($\bar{x}$ = 19.98)
Distance between posterior borders of eyes in % of head height		85.2–110.1 ($\bar{x}$ = 95.49)		70.9–107.6 ($\bar{x}$ = 84.9)
Length of 4th toe nail in % of width of 5 ventral scales (♂♂ only)		20.5–38.6 ($\bar{x}$ = 30.02)		31.6–50 ($\bar{x}$ = 40.81)
Distance between the pubic symphysis and the vent as % of ear–eye distance (♀♀ only)		80–124 ($\bar{x}$ = 98.84)		62–99 ($\bar{x}$ = 78.65)

TABLE 3. Continued.

	robustus (N = 15)	*polystictus* (N = 17)	*williamsi* (N = 15)	*signifer* (=*multiformis*) (N = 32)
Minimum distance between nasals in % of minimum distance between supraocular scales	90–142 ($\bar{x}$ = 113.31)	56–87 ($\bar{x}$ = 70.8)	65–139 ($\bar{x}$ = 95.7)	
Rostral height in % of eye–lip distance	43–65 ($\bar{x}$ = 50.57)	50–74 ($\bar{x}$ = 60.62)	48–62 ($\bar{x}$ = 55.85)	
Length of 5 dorsal scales in % of ear–eye distance			67–104 ($\bar{x}$ = 79.4)	29–71 ($\bar{x}$ = 49.58)
Eye–lip distance in % of subocular length	47–70 ($\bar{x}$ = 54.83)		37–58 ($\bar{x}$ = 49.05)	
Length of 1st finger (without claw) in % of length of 5 dorsal scales		51–83 ($\bar{x}$ = 65.95)	40–65 ($\bar{x}$ = 54.14)	

the norm for the entire genus *Liolaemus,* but the other features might characterize a valid subspecies if confirmed for a majority of the specimens from the region.

Relationships. All of these specimens had been identified as *L. multiformis* (Cope). However, they are clearly different from the syntypes of the species and series collected around Lake Titicaca. The most obvious differences are indicated in Table 3 and Figure 1.

There is also a large and clear-cut morphometric difference: the width of the frontal region at its narrowest point is less than 25% of the length of 5 dorsal scales (lowest value 13%) in *robustus*; in *signifer* the same measurement is more than 25% (highest value 48.9%). The name of the species has been inspired by its robust appearance. While it is expected to be most significant in this respect, the width of head/snout–vent length ratio is not diagnostic at all: 18.31 to 24.57% (mean = 21.73%) in *robustus* versus 18.78 to 22% (mean = 20.54%) in *signifer* (see Fig. 2).

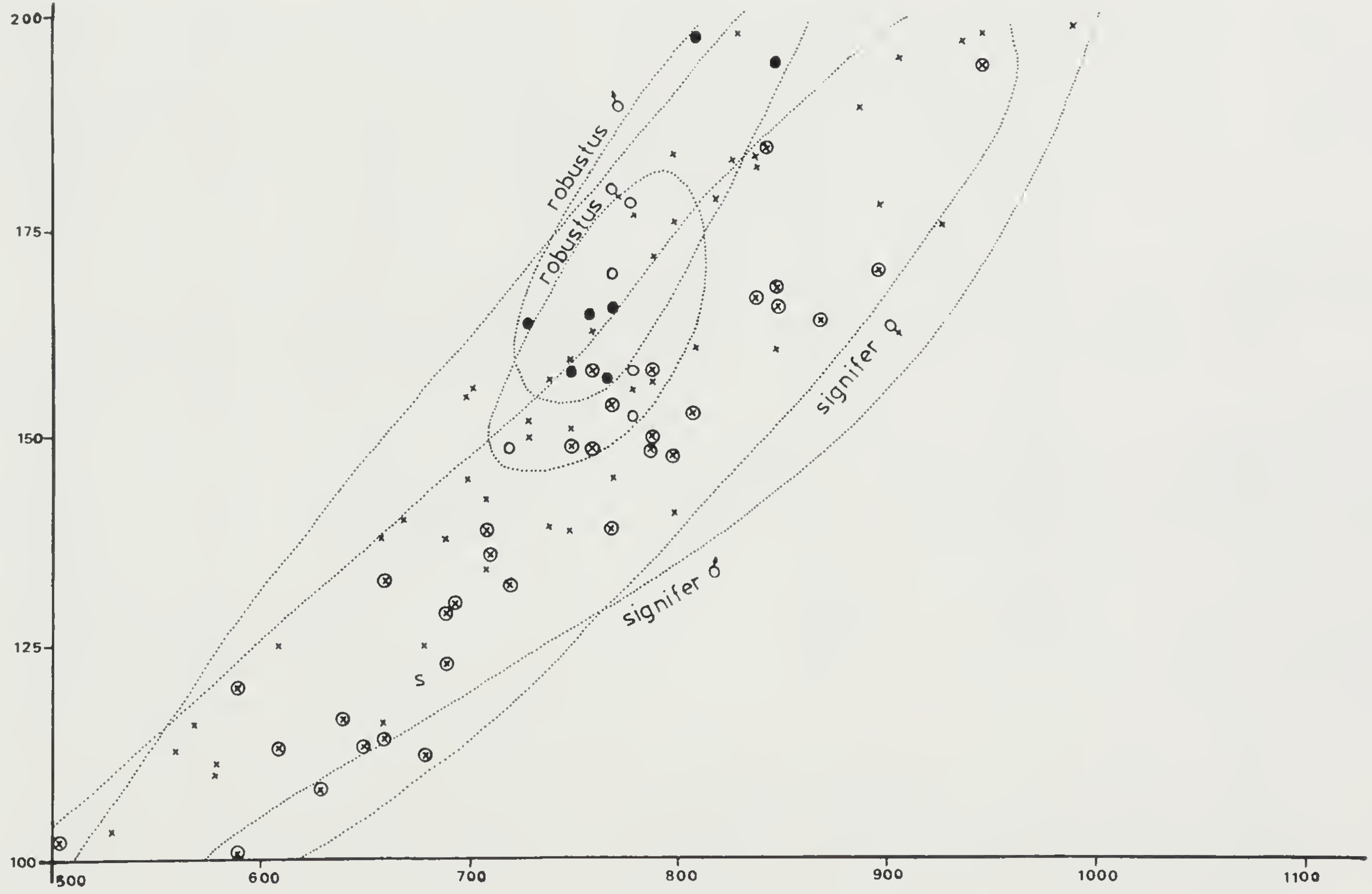

Figure 2. Scatter-diagram of width of head (ordinates) and snout–vent length (abscissa). Measurements in tenths of a millimeter. ● = *Liolaemus robustus* ♂, and ○ = ♀. × = *L. signifer* ♂, and ⊗ = ♀. S = Type of *L. signifer*.

L. robustus, as well as the two new species described below, is not compared here with other *Eulaemus* species. Other papers, which will remedy this lack, are in preparation. They include descriptions of other new species, one from Peru, one from northern Chile, and 5 from northwestern Argentina, and the last of the series is intended to provide a key to all *Eulaemus* without enlarged femoral scales.

The sexual dimorphism of *L. robustus* is not as conspicuous as that of *L. signifer.* The size difference is less marked, and the color pattern is about the same in both sexes, at least in alcohol. However, the colors in life are probably brighter in males than in females.

Liolaemus polystictus, new species
(Pl. III, Figs. 1–4; Pl. II, Figs. 1–2)

Holotype. One male (MCZ 45845) from Santa Inez (13°12′S, 75°05′W), about 100 km S of Huancavelica, Depto. Huancavelica, Peru, W. F. Walker Sr., collected February 1939.

Paratypes. PERU: *Depto. Huancavelica:* Same data as holotype: 2 males MCZ 45844, 45846, 3 females MCZ 45847–49, 2 juveniles MCZ 161157–58, 1 male, 1 female UMMZ 89482. Same locality and collector: MCZ 43782, collected 14 December 1936. Huancavelica: 5 males, 4 females, 2 juveniles FNHM 81453–63, no collector, no date. Six km SW Castrovirreyna, 3,650 m, KU 163563, W. E. Duellman, collected 24 February 1975.

Diagnosis. A species of the *Liolaemus signifer* group, differing from all other members of this group by the male color pattern, in which each dorsal scale is bicolor, pigmented at the base, clear behind, giving a striking appearance of fine punctation, and by having a greater sexual dimorphism in size.

It can be distinguished from *L. signifer* by the following differences: 1) 62–75 ventral scales instead of 74–92 between postmentals and vent; 2) 57–70 scales instead of 66–82 around midbody; 3) 55–70 dorsal scales instead of 65–87 between occiput and level of front borders of thighs; 4) some morphometric differences only noticeable on scatter-diagrams because of allometry (Figs. 3–5).

L. polystictus differs from *L. robustus* in the following characters: 1) minimum width of frontal region 24–38% of length of 5

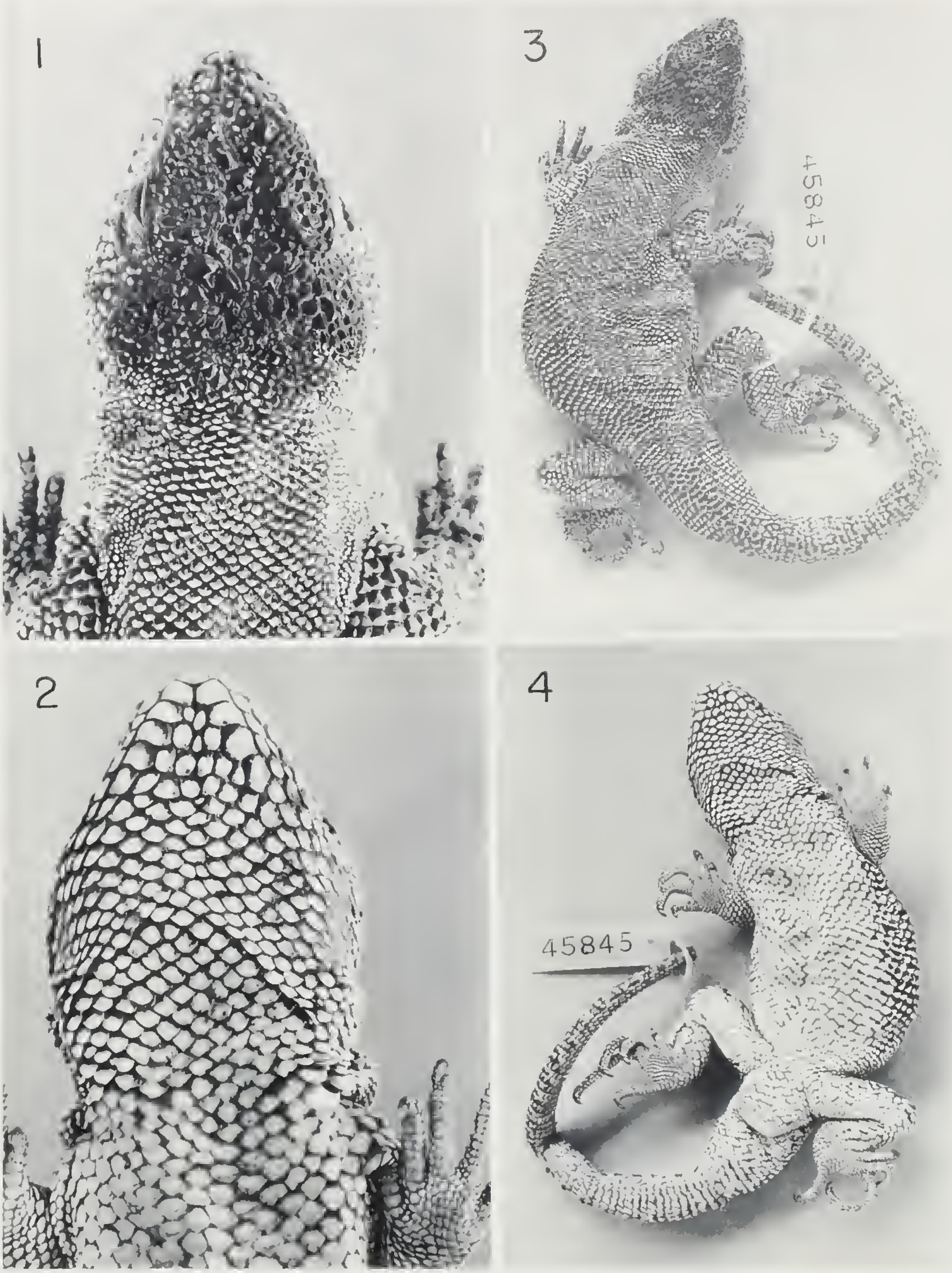

Plate III. *Liolaemus polystictus,* sp. nov. Holotype male: MCZ 45845. Huancavelica, Peru. 1. Dorsal view of head. 2. Ventral view of head. 3. Dorsal view. 4. Ventral view.

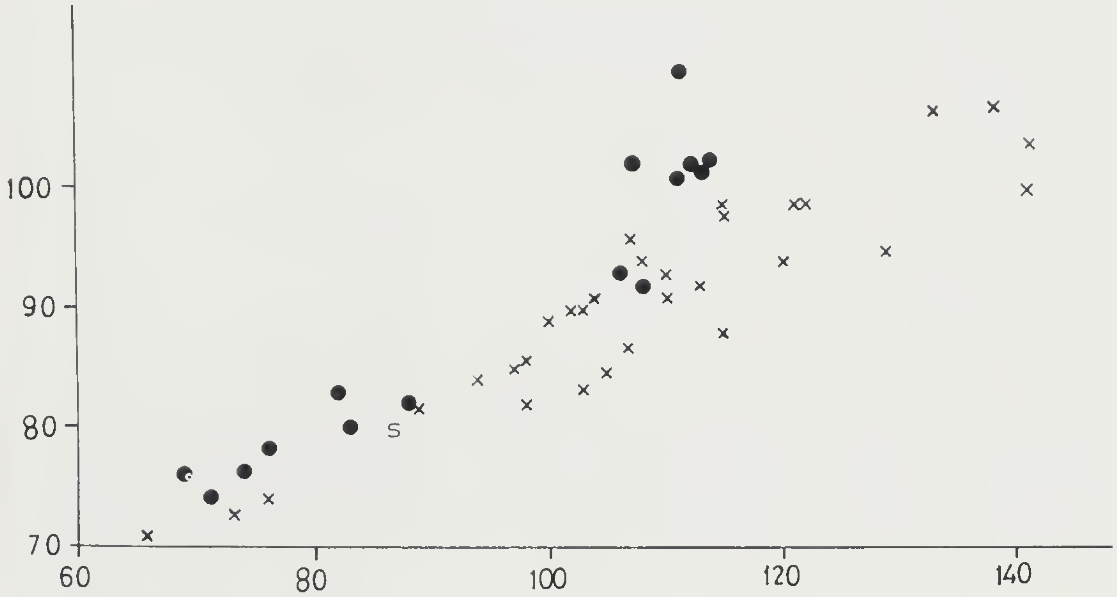

Figure 3. Scatter-diagram of distance between posterior eye borders (ordinates) and head height (abscissa). Measurements in tenths of a millimeter. ● = *Liolaemus polystictus,* sp. nov. × = *L. signifer.* S = Type of *L. signifer.*

dorsal scales instead of 13–23% (see Fig. 1); 2) minimum distance between nasals 56–87% of minimum distance between supraocular scales instead of 90–142%; 3) 57–70 scales around midbody instead of 47–61; 4) 55–70 dorsal scales instead of 44–59 between occiput and level of front borders of thighs.

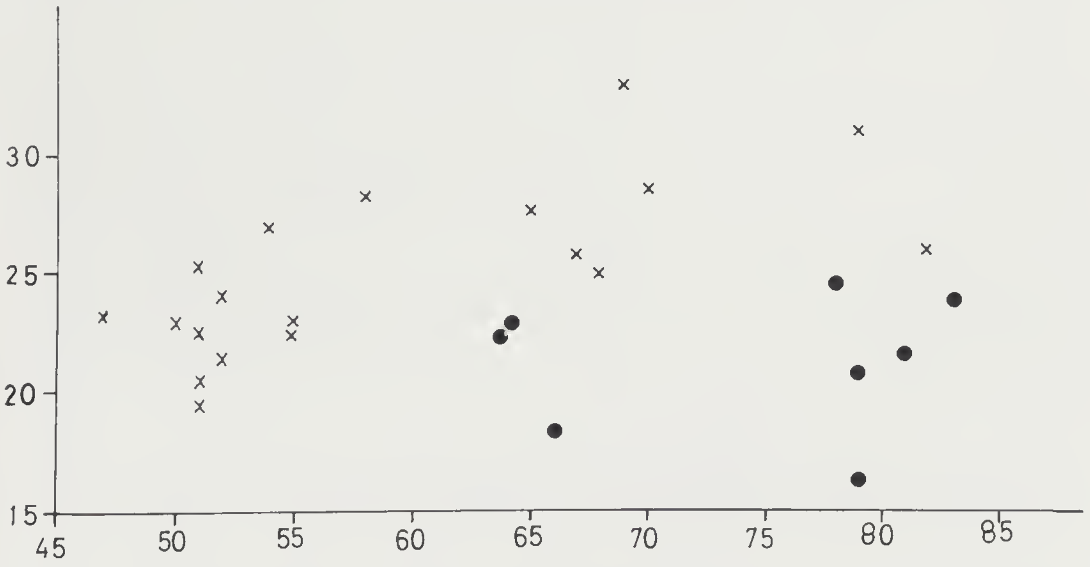

Figure 4. Scatter-diagram of length of claw of 4th toe (ordinates) and width of 5 ventral scales (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus signifer.* ● = *L. polystictus,* sp. nov. Males only.

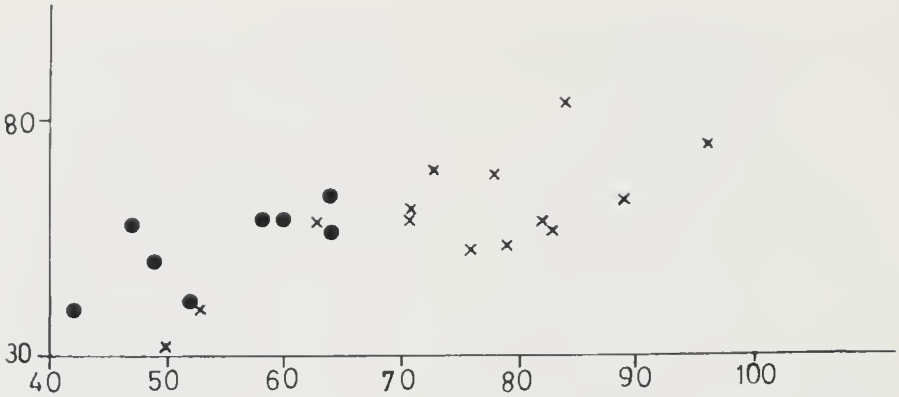

Figure 5. Scatter-diagram of distance between armpit and groin (ordinates) and ear–eye distance (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus signifer*. ● = *L. polystictus*, sp. nov. Females only.

Description of the Holotype. Head length (from posterior rim of ear opening) (HL = 22 mm) 28.9% of snout–vent length (SVL = 76 mm). Vertical lateral folds of the neck overshadowed by a horizontal fold, which is sinuous and bifurcated just behind the ear. Scales on upper surface of head strongly convex, 16 on the midline. Temporals convex, some slightly keeled, keels higher behind than in front, 8–9 between the postsubocular and the ear. Frontal region occupied by two azygous scales, their front and rear borders oblique, five supraoculars. Rostral plate 2.76 times wider (WR = 4 mm) than high (HR = 1.45 mm). Nasal triangular, separated from rostral, surrounded by 8 scales, nostril in the posterior part of nasal, nearer to point of snout (NS = 2.95 mm) than to hind border of canthal scale (NC = 3.7 mm). Internasals: 4 anterior + 4 posterior, all irregular. Ear opening oval and oblique, surrounded by granular scales, smaller behind than in front of the ear. Eight to seven supraciliaries, the 5th lateral to the others on the left, the 4th and 5th on the right. Six scales between the rostral and the frontal region. Five scales between the frontal region and the supraciliaries.

The prefrontal zone between the posterior internasals and the frontal region contains 13 scales, rather irregularly arranged. Five intercanthal scales. Across the snout between the supralabials 12 scales behind the postnasal level, 14 at the canthal level. Four scales between the nasal and the subocular. Paralabials 9–7, 5–3 in contact with subocular.

Table 4. Meristic characters in *Liolaemus polystictus*, sp. nov. (9 ♂♂, 8 ♀♀, juveniles not included).

	♂♂	♀♀
Scales around midbody	57–70 ($\bar{x}$ = 61.34)	63–68 ($\bar{x}$ = 64.87)
Dorsal scales between occiput and level of anterior border of thigh	55–63 ($\bar{x}$ = 59.22)	57–70 ($\bar{x}$ = 62.62)
Ventral scales between postmentals and vent	62–67 ($\bar{x}$ = 64.67)	64–75 ($\bar{x}$ = 68.12)
Lateral scales between legs	54–70 ($\bar{x}$ = 62.78)	53–76 ($\bar{x}$ = 63.75)
Scales in 15th verticil of tail	17–20 ($\bar{x}$ = 19.40)	19–22 ($\bar{x}$ = 20.87)
Gular scales between ears	27–32 ($\bar{x}$ = 29.56)	28–32 ($\bar{x}$ = 29.88)
Hellmich's index	16–21 ($\bar{x}$ = 17.78)	14–21 ($\bar{x}$ = 18.38)
Lamellae under 4th finger	17–18 ($\bar{x}$ = 17.67)	15–19 ($\bar{x}$ = 16.25)
Lamellae under 4th toe	20–24 ($\bar{x}$ = 21.56)	19–22 ($\bar{x}$ = 20.5)

Nine supralabials on the left side, 8 on the right side. Seven to six infralabials, followed by 6–7 granules as far as the corner of the mouth. Mental fan-shaped, in contact with 4 scales.

Lateral scales of the neck granular, 41 between ear opening and front leg, 32 scales between ear openings, 63 scales around the body, 61 between occiput and level of front border of thighs. Dorsal scales imbricate and keeled. Lateral scales smaller, erect and granular, smaller still at armpit and groin, 58 between legs. Ventral scales smooth and imbricate, 63 between mental and preanal pores. Five preanal pores. Caudal scales similar to body scales, 20 in 15th verticil of tail. Seventeen subdigital lamellae beneath 4th finger, 22 beneath 4th toe.

Color (in Alcohol). Above, blackish with a very dense and fine punctation resulting from the fact that each dorsal scale is pigmented at the base, unpigmented at the tip. Below, the belly is light, with black pigmentation on the borders of the scales, which gives a reticulate appearance especially marked on the throat. On the lateral scales, the pigmented and unpigmented areas are about equal, so that the general effect is checkered. Upper surface of head blackish.

The color in life is unknown, but it is surmised that the unpigmented parts are actually vividly colored (white, yellow, orange, red, green, or blue).

Variation (see Table 4). Upper labials generally 9 (15 sides), sometimes 8 (6 sides) or 10 (5 sides), rarely 6–7 (1 side each) or 11 (4 sides), the first 5 to 8 without small scales below and inside. Lower labials generally 5 (14 sides) or 6 (12 sides), sometimes 7 (5 sides), rarely 4 (1 side). Supraoculars generally 5 (15 sides), sometimes 4 (8 sides), rarely 3 (3 sides), 6 (5 sides) or 7 (1 side). In one individual, only one plate on the left and two on the right are enlarged enough to be termed supraoculars. Supraciliaries as usual 7, the 5th below the 4th and the 6th, at least in females, except in one case where the number is 6, but anomalies are surprisingly common in males, where 6 is actually the most frequent number (9 sides), while 7 is less common (5 sides), 5 (2 sides) and 8 (1 side) are rare; the lower supraciliary, which is generally the 5th, is the 4th on 4 sides (3 in males). Three males each show another anomaly on one side: 1) the 5th supraciliary is in front of the 6th, not below; 2) the 3rd supraciliary is also below the 2nd and the 4th; 3) the 4th and the 5th supraciliaries are both overhung by the 3rd and the 6th. Temporals between the postsubocular and the ear usually 8 (10 sides) or 9 (9 sides), often 7 (8 sides, 6 sides in females), rarely 10 (3 sides, all in females) or 6 (3 sides), exceptionally 5 (1 side in a male). Plates between the rostral and the frontal most often 6 (16 sides), less often 5 (12 sides), sometimes 7 (6 sides). Scales between the frontal and the supraciliaries 5, sometimes 4 (9 sides) mostly in females (8 sides), exceptionally 3 (1 side). Scales around the interparietal usually symmetrical (irregular in only 4 specimens), usually 6 (9 specimens), sometimes 7 (5 cases) or 8 (3 cases). Scales around the nasal generally 7 (20 sides), sometimes 6 (7 sides, 2 in males) or 8 (6 sides, 5 in females), rarely 9 (1 side), rarely including the rostral (2 sides). Paralabials usually 9 (18 sides), sometimes 8 (13 sides), rarely 7 (3 sides). Paralabials in contact with subocular generally 4 (15 sides), sometimes 5 (10 sides) or 3 (9 sides). Plates between the upper labials around the snout behind nasals 7–13 (mean = 10.6), 10–15 at the canthal level (mean = 12.25). Scales between nasal and subocular usually 4, rarely 5 (7 sides) or 6 (2 sides); in this last case, the subocular is actually divided, which is a presumed return to a primitive condition. Preanal pores 5 (6 specimens), 4 (2 specimens), or 3 (1 specimen). In frontal, always at least one azygous element, most often 2 (7 cases), only single

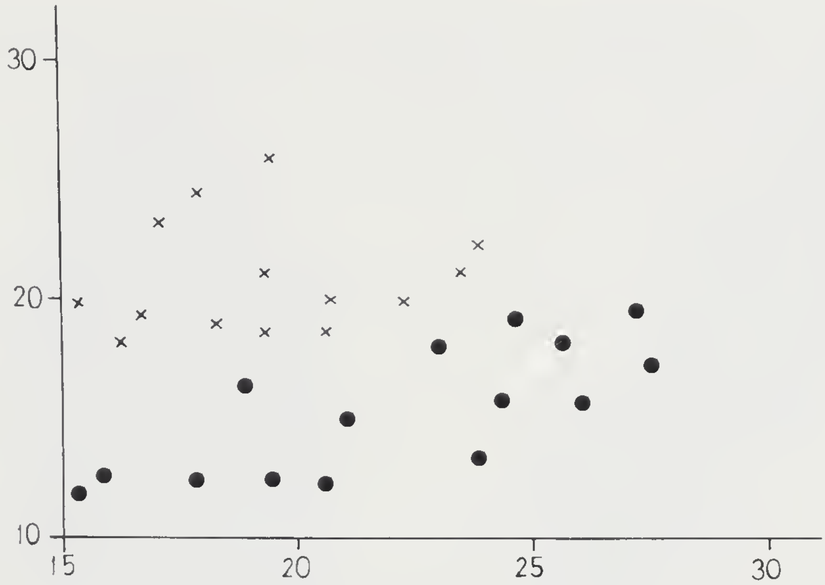

Figure 6. Scatter-diagram of minimum distance between nasals (ordinates) and minimum distance between supraoculars (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus robustus,* sp. nov. ● = *L. polystictus,* sp. nov.

(frontal undivided) in one case, 3 in a longitudinal line (1 case), 3 with 2 in front (2 cases), 3 with 2 behind (2 cases), 3 with 2 laterals (1 case), 4 with 2 in front and 2 longitudinally behind (1 case), 5 with 2 in front, 2 behind and 1 central (2 cases).

The color pattern of males hardly varies at all; the fine and regular dorsal punctation and the ventral reticulation are always

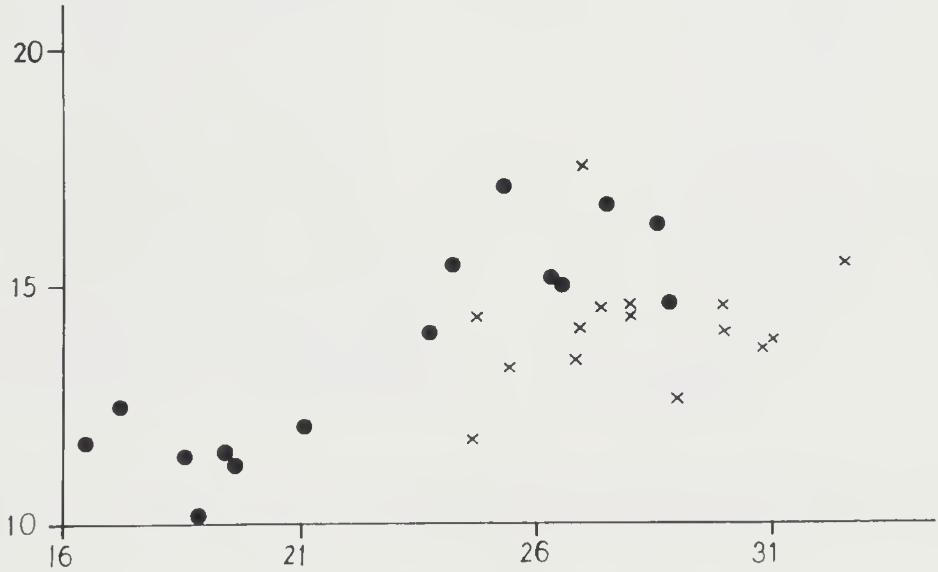

Figure 7. Scatter-diagram of rostral height (ordinates) and distance between subocular upper border and mouth (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus robustus.* ● = *L. polystictus,* sp. nov.

present but are obscured in the specimens belonging to the Field Museum of Natural History, presumably because of too long an exposure to formalin. The females and the young are gray to reddish brown (in alcohol) with the usual two latero-dorsal series of blackish blotches.

Habitat. The only information we have is that of W. E. Duellman, who found the juvenile paratype under a rock in a grassy river valley.

Size. Snout–vent length of the largest male 86 mm (tail 102 mm), of the largest female 69 mm (tail 77 mm).

Systematic Position. Both *L. robustus* and *L. polystictus* are vicariants of *L. signifer.* They are considered different species because they are well-differentiated and separated by mountainous barriers that must have interrupted any gene flow over a long period of time.

The most obvious differences between *L. polystictus* and *L. signifer* are the color pattern, and the great disparity in size between the sexes in the former.

There are other characters. The frontal in *L. polystictus* is more often divided than in *L. robustus* but less than in *L. signifer.* A similar intermediacy is apparent in scale numbers (see Table 3) except for the ventral longitudinal counts that are even lower, although very slightly, in *polystictus* than in *robustus.*

Morphometrically, *L. polystictus* is more similar to *signifer* than to *robustus* in some respects but more similar to *robustus* in others (width of head).

The pertinent data are indicated in Table 3, but the ratios somewhat understate the differences because of allometric distortions. The scatter-diagrams give a better idea of the character differences (see Figs. 3–7).

Liolaemus williamsi, new species
(Pl. IV, Figs. 1–4)

Holotype. One male (LACM 9323), Pampas Galeras, between Nazca and Puquio, Depto. Ayacucho, Peru, x-1965, coll. S. W. Taft.

Paratypes. Four males, 3 females, 2 juveniles (LACM 9319–22, 9324–28), same data. Four males, 3 females, 3 juveniles (LACM 9329–38), Lucanas, Pampas Galeras, 96 km from Nazca,

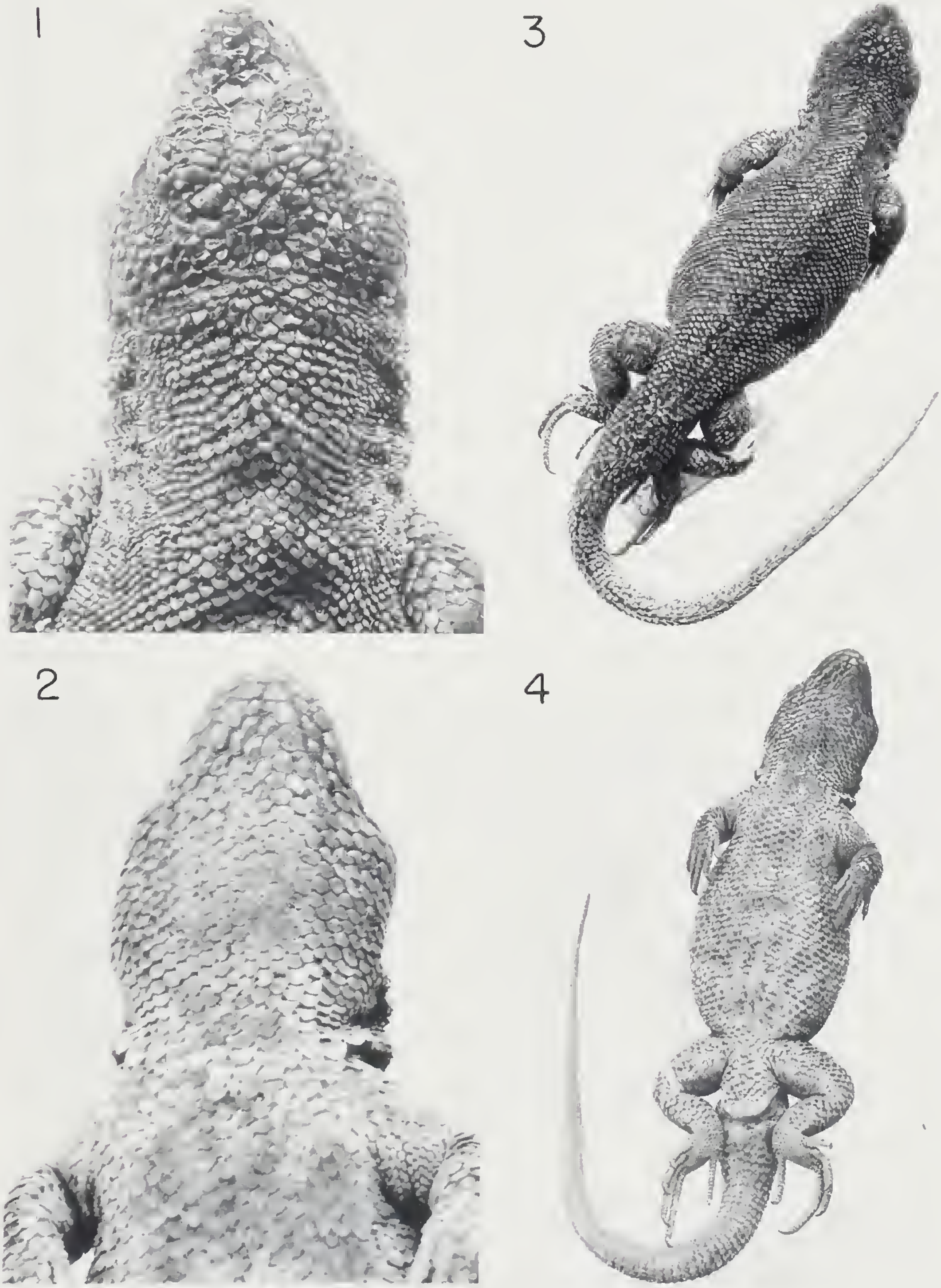

Plate IV. *Liolaemus williamsi,* sp. nov. Holotype male: LACM 9323. Pampas Galeras, Depto. Ayacucho, Peru. 1. Dorsal view of head. 2. Ventral view of head. 3. Dorsal view. 4. Ventral view.

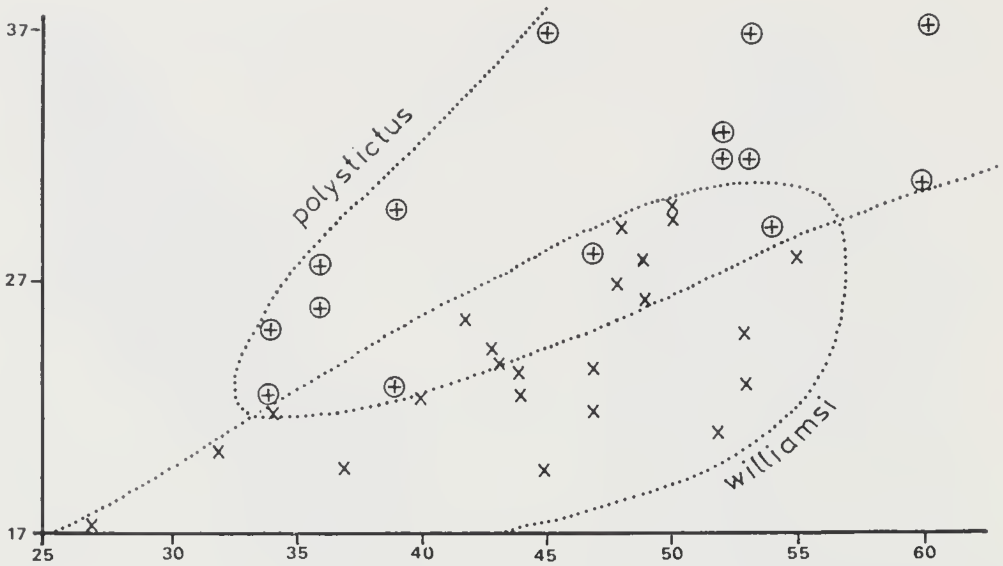

Figure 8. Scatter-diagram of length of the first finger, without claw (ordinates) and length of 5 dorsal scales (abscissa). Measurements in tenths of a millimeter. × = *L. williamsi.* ⊕ = *L. polystictus.*

Depto. Ayacucho, Peru, iv–vii-1963, coll. S. W. Taft. One female (LACM 35867), Pampas Galeras, 300 miles south of Lima, Depto. Ayacucho, Peru, iii-1966, coll. S. W. Taft. One male (MCZ 100435), Lucanas, Pampas Galeras, Depto. Ayacucho, Peru. One male, 2 females, 4 juveniles (MCZ 145335–41), Reserva Nacional de Pampas Galeras, 90 km from Nazca, Depto. Ayacucho, 21, iv-1974, coll. R. A. Mittermeier. One female (MCZ 157223), Pampas Galeras, Lucanas (exch. Mus. Javier Prado).

Diagnosis. A middle-sized and somewhat melanistic species of the *L. signifer* group, differing from *L. signifer* by its larger and less numerous scales and the presence of preanal pores in some females.

It differs from *L. signifer* in the following features: 1) 54–67 scales around midbody instead of 66–82; 2) 48–65 dorsal scales instead of 65–87 between occiput and level of front borders of thighs; 3) 67–78 ventral scales instead of 74–92 between postmentals and vent; 4) minimum width of frontal region 18–29% of length of 5 dorsal scales instead of 25–49%; 5) length of 5 dorsal scales 67–104% of ear–eye distance instead of 29–71%.

It can be distinguished from *L. robustus* by the following differences, apart from color pattern: 1) 66–77 lateral scales between

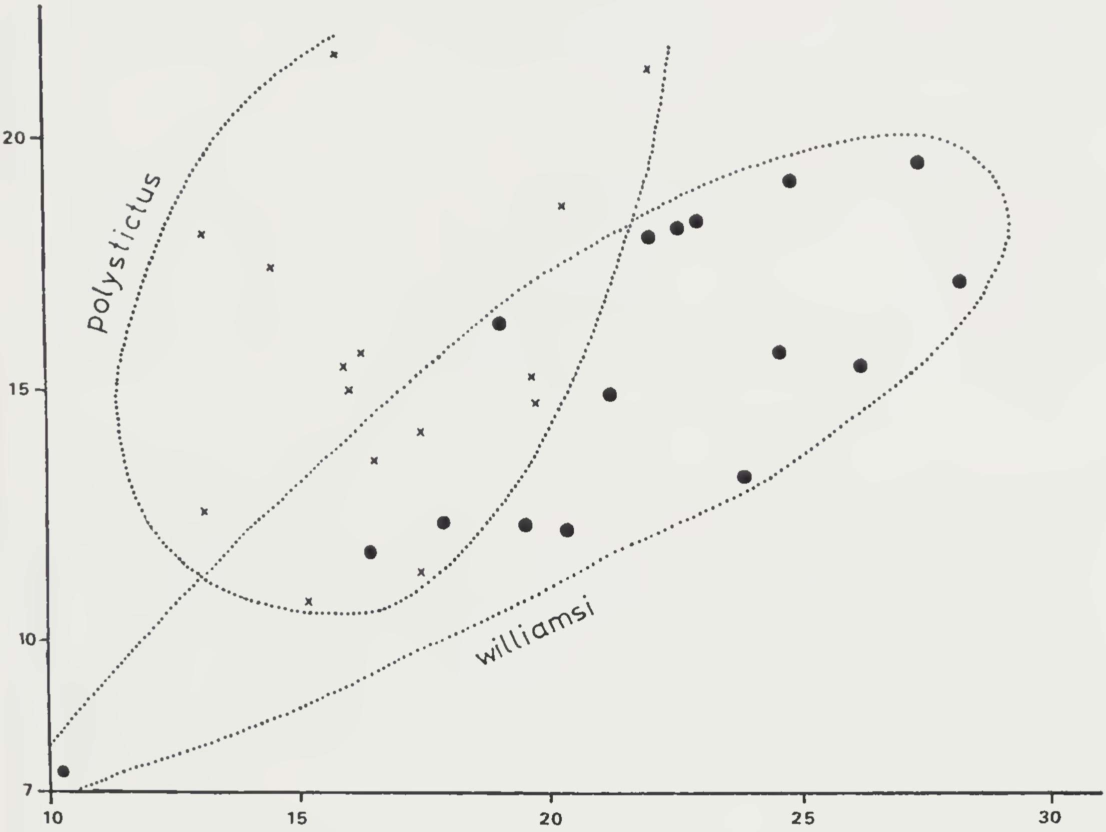

Figure 9. Scatter-diagram of minimum distance between nasals (ordinates) and minimum distance between supraoculars (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus polystictus*, sp. nov. ● = *L. williamsi*. The difference is essentially allometric.

legs instead of 49–70; 2) 17–22 dorsal scales instead of 12–19 in head length.

It differs from *L. polystictus* by the larger number of ventral scales between postmentals and vent (67–78 instead of 62–71) and several morphometric characters mostly noticeable only on scatter-diagrams (Figs. 8, 9).

Description of the Holotype. Head length (HL = 19.2 mm) 25.6% of snout–vent length (SVL = 75 mm). Vertical lateral folds of the neck overshadowed by a horizontal and sinuous fold bifurcated in front. Scales on upper face of head convex, 15 on the midline. Rostral plate 2.87 times wider (WR = 3.7 mm) than high (HR = 1.29 mm). Nasal more or less trapezoidal, surrounded by 6 scales. Nostril round, in the posterior part of nasal, nearer to point of snout (NS = 2.55 mm) than to hind border of canthal scale (NC = 2.89 mm). Two anterior and 4 posterior internasals.

TABLE 5. MERISTIC CHARACTERS IN *LIOLAEMUS WILLIAMSI*, SP. NOV. (11 ♂♂, 11 ♀♀, JUVENILES NOT INCLUDED).

	♂♂	♀♀
Scales around midbody	54–64 ($\bar{x}$ = 59)	57–67 ($\bar{x}$ = 60.09)
Dorsal scales	48–62 ($\bar{x}$ = 54.64)	49–65 ($\bar{x}$ = 57.82)
Ventral scales	67–77 ($\bar{x}$ = 70.82)	71–78 ($\bar{x}$ = 74.55)
Lateral scales	66–75 ($\bar{x}$ = 70.36)	66–77 ($\bar{x}$ = 72.36)
Scales of tail's 15th verticil	17–21 ($\bar{x}$ = 19.36)	18–22 ($\bar{x}$ = 19.36)

Ear openings oval and very slightly oblique, surrounded by granular scales smaller behind than in front. Temporals convex, smooth, and slightly imbricate, 6–7 between the postsubocular and the ear. Frontal region occupied by 2 azygous scales. Six supraoculars, 7 or 6 supraciliaries, the 5th or 4th below the 4th and 6th or the 3rd and 5th. Five to six scales between the rostral and the frontal. Five scales between the frontal and the superciliaries.

In prefrontal zone, between the posterior internasals and the anterior frontal, 12 scales, more or less symmetrically arranged. Four intercanthal scales. Across the snout, between left and right labials, 11 scales just behind the postnasal level, 11 also at the canthal level. Four or 5 scales between nasal and subocular. Paralabials 8–9, 5 in contact with the subocular.

Supralabials 8–9. Infralabials 5, followed by 6–7 granules as far as the corner of the mouth. Mental fan-shaped, in contact with 4 scales.

Lateral scales of neck granular, 46 between ear and fore limb. Thirty-three scales between ear openings. Fifty-nine scales around body. Fifty between occiput and level of insertion of thighs.

Dorsal scales imbricate and keeled. Lateral scales smaller, imbricate and feebly keeled, still smaller at axilla and groin. Seventy-two scales between legs. Ventral scales smooth and imbricate, 68 between mental and preanal pores. Four preanal pores. Caudal scales similar to body scales, 17 in the 15th verticil. Sixteen subdigital lamellae under 4th finger, 20 beneath 4th toe.

Color (in Alcohol). Blackish with numerous tiny gray dots (one on each scale). Below, darkish gray, with light areas on cloacal region and thighs.

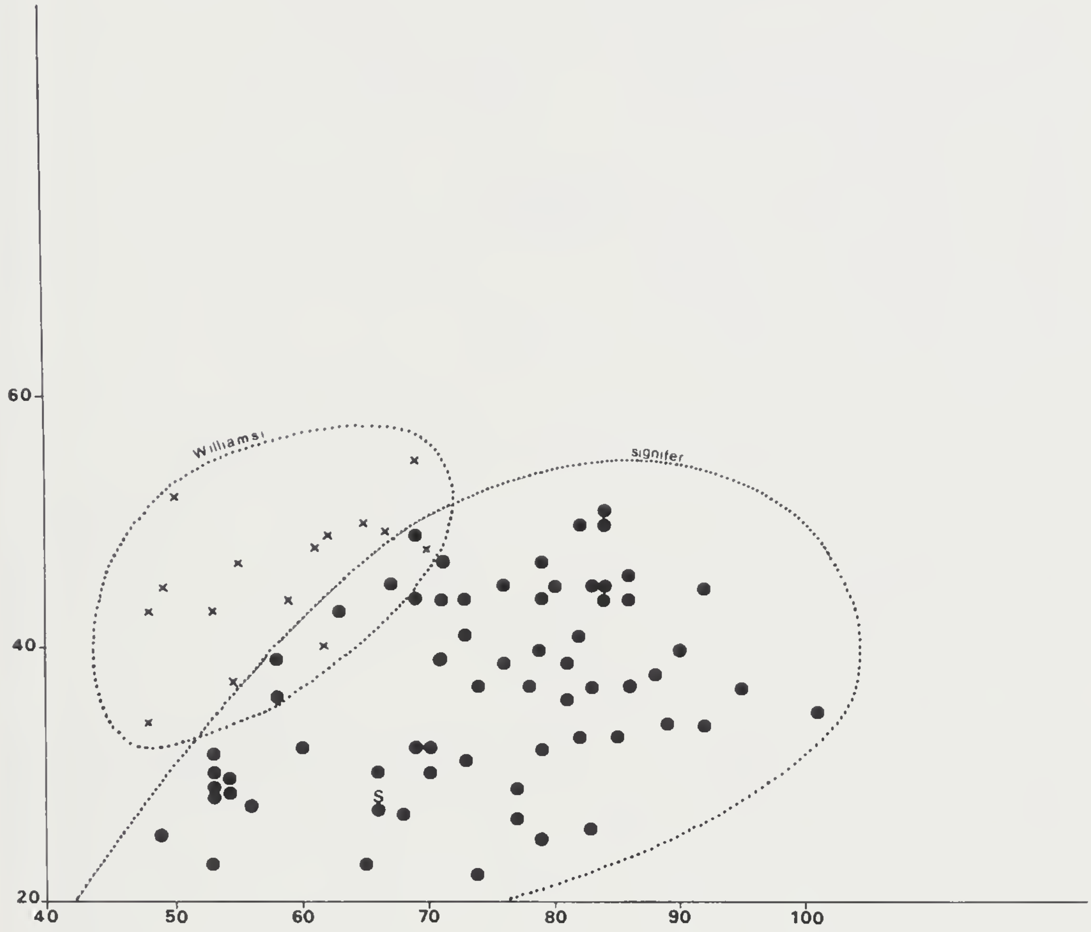

Figure 10. Scatter-diagram of length of 5 dorsal scales (ordinates) and ear–eye distance (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus williamsi*. ● = *L. signifer*. S = Type of *L. signifer*.

Color (in Life). Unknown.

Variation (see Table 5). Upper labials generally 8 (18 sides) or 9 (20 sides), sometimes 10 (9 sides), rarely 7 (2 sides), 11 (1 side) or 12 (1 side), the first 4 to 8 without small scales below and inside. Lower labials generally 6 (26 sides) or 5 (21 sides), rarely 7 (4 sides) or 4 (1 side). Supraoculars generally 5 (30 sides), sometimes 6 (15 sides) or 4 (9 sides), rarely 3 (1 side) or 7 (1 side). Supraciliaries as usual 7, the 5th below the 4th and 6th, but anomalies are frequent: 6 (5) (5 sides), 6 (4) (1 side), 8 (6) (3 sides), 8 (5) (1 side), 9 (6) (1 side), or 8 (4 and 6) (1 side), 6 (0) (1 side).

Temporals between postsubocular and ear generally 7 (32 sides), sometimes 8 (9 sides) or 6 (7 sides), rarely 9 (4 sides). Scales between rostral and frontal most often 5 (27 sides), less often 6 (20 sides), rarely 7 (3 sides), 4 (1 side) or 8 (1 side). Scales between

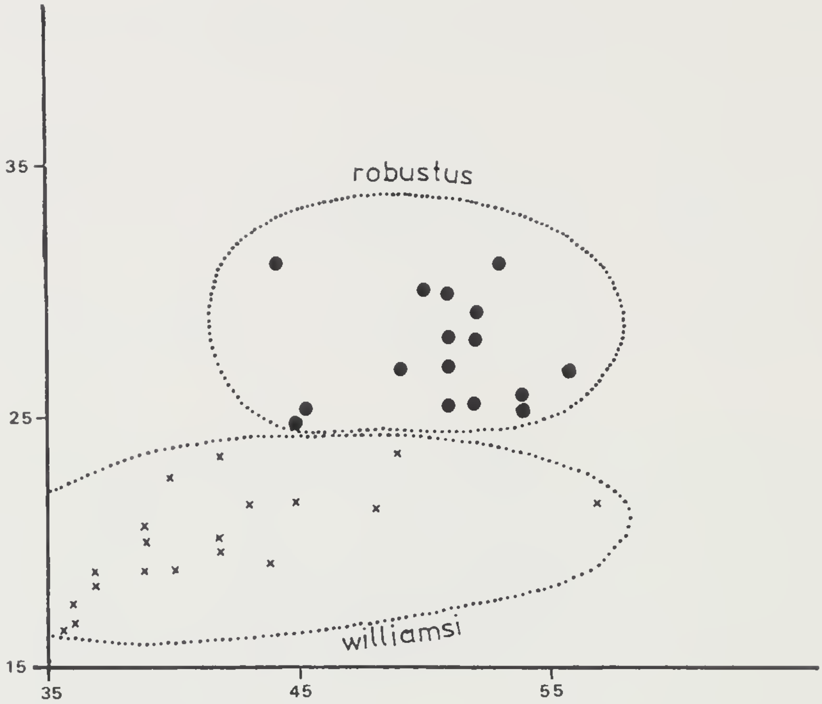

Figure 11. Scatter-diagram of minimum distance between upper border of subocular and lip (ordinates) and supraocular length (abscissa). Measurements in tenths of a millimeter. ● = *L. robustus.* × = *L. williamsi.*

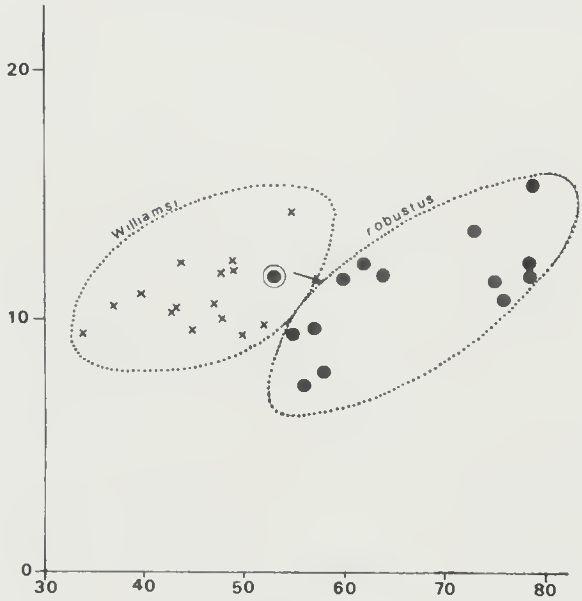

Figure 12. Scatter-diagram of minimum width of the frontal region (ordinates) and length of 5 dorsal scales (abscissa). Measurements in tenths of a millimeter. × = *Liolaemus williamsi,* sp. nov. ● = *L. robustus,* sp. nov.

frontal and supraciliaries normally 4 (29 sides), often 5 (19 sides), rarely 3 (5 sides), exceptionally 2 (1 side). Scales around the interparietal often asymmetrical (13 cases), most often 7 (13 cases), sometimes 8 (7 cases), rarely 9 (3 cases) or 6 (3 cases), exceptionally 10 (1 case). Scales around nasal normally 6 (33 sides), sometimes 7 (13 sides), rarely 5 (2 sides) or 8 (3 sides). Paralabials most often 8 (23 sides), often 7 (13 sides) or 9 (14 sides), rarely 6 (1 side) or 10 (1 side). Paralabials in contact with subocular generally 4 (22 sides), often 3 (13 sides) or 5 (11 sides), rarely 2 (3 sides) or 6 (1 side). Scales between supralabials 8–14 at the postnasal level (mean = 10.75), 11–15 (mean = 12.53) at the canthal level. Preanal pores, 5 in 5 males, 4 in 4 males, 6 in 2 males, present also but poorly developed in some females. Frontal not divided in 1 case, divided into 2 median scales in 12 cases, into 4 symmetric scales in 1 case, into 5 scales symmetrically arranged (2 anterior, 1 azygous, 2 posterior) in 2 cases, into 5 scales with the azygous posterior in 1 case, into 3 scales with the azygous one posterior in 2 cases, into 3 scales with the azygous one anterior in 2 cases.

Tail, when not broken or regenerated, longer than snout–vent length, 127 to 138.5% (mean = 131.45%).

Size. Largest male 76 mm SVL, largest female 77 mm SVL.

Color (in Alcohol). In males, as shown by specimens other than the holotype, the color is generally blackish, sometimes with light markings that can fuse and form more or less oblique and discontinuous transverse lines. In one specimen, the color is lighter and allows about 14 pairs of blackish spots to be seen. The belly can be light with a few black dots, but is more often dark with a few light areas or spots. In females and juveniles the two longitudinal series of dark blotches on a light background are distinct. The belly is light with dark markings.

L. williamsi differs from *L. signifer, L. robustus,* and *L. polystictus* by its smaller size and dark coloration (possibly artificial in some specimens), the presence of preanal pores in some females, the frequencies of its meristic characters, and some of its proportions (see Table 3 and Figs. 8–12). As described above, the species represents the differentiation of populations of relatively smaller size in the upper parts of Pacific Andean valleys isolated from larger-size populations of the Altiplano.

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APPENDIX

Subgenus *Liolaemus*	Subgenus *Eulaemus*
	signifer group
L. alticolor Barbour 1909	*L. andinus*
L. atacamensis Müller & Hellmich 1933	*a. andinus* Koslowsky 1895 *a. poecilochromus* Laurent 1986
L. austromendocinus Cei 1974	*L. aymararum* Veloso, Sallaberry,

APPENDIX. Continued.

Subgenus *Liolaemus*

- *L. bellii*
  - *b. bellii* Gray 1845
  - *b. araucaniensis* Müller & Hellmich 1932
  - *b. moradoensis* Hellmich 1950
  - *b. neuquensis* Müller & Hellmich 1938
- *L. bibronii* Bell 1843
- *L. bisignatus* Philippi 1860
- *L. bitaeniatus* Laurent 1984
- *L. buergeri* Werner 1907
- *L. capillitas* Hulse 1979
- *L. ceii* Donoso-Barros 1971
- *L. chiliensis* Lesson 1828
- *L. coeruleus* Cei & Ortiz 1983
- *L. constanzae* Donoso-Barros 1961
- *L. copiapensis* Müller & Hellmich 1933
- *L. curicensis* Müller & Hellmich 1938
- *L. curis* Nuñez & Labra 1985
- *L. cyanogaster*
  - *c. cyanogaster* Duméril & Bibron 1837
  - *c. brattstroemi* Donoso-Barros 1961
- *L. donosoi* Ortiz 1975
- *L. duellmani* Cei 1978
- *L. elongatus*
  - *e. elongatus* Koslowsky 1896
  - *e. petrophilus* Donoso-Barros & Cei 1971
- *L. exploratorum* Cei & Williams 1984
- *L. fitzgeraldi* Boulenger 1899
- *L. fuscus* Boulenger 1885
- *L. gracilis* Bell 1843
- *L. gravenhorstii* Gray 1845
- *L. hellmichi* Donoso-Barros 1974
- *L. hernani* Sallaberry, Nuñez & Yañez 1982
- *L. kriegi* Müller & Hellmich 1939
- *L. kuhlmanni* Müller & Hellmich 1932

Subgenus *Eulaemus*

signifer group

Navarro, Iturra, Valencia, Penna & Diaz 1982

- *L. disjunctus* Laurent 1990
- *L. dorbignyi* Koslowsky 1898
- *L. eleodori* Cei, Etheridge & Videla 1985
- *L. fabiani* Yañez & Nuñez 1983
- *L. famatinae* Cei 1980
- *L. fittkaui* Laurent 1986
- *L. forsteri* Laurent 1982
- *L. griseus* Laurent 1984
- *L. huacahuasicus* Laurent 1985
- *L. islugensis* Ortiz & Marquet 1987
- *L. jamesi* Boulenger 1891
- *L. montanus* Koslowsky 1898
- *L. multicolor* Koslowsky 1898
- *L. nigriceps* Philippi 1860
- *L. orientalis* Müller 1923
- *L. ortizi* Laurent 1982
- *L. polystictus* Laurent 1991
- *L. puritamensis* Nuñez & Fox 1989
- *L. robustus* Laurent 1991
- *L. ruibali* Donoso-Barros 1961
- *L. schmidti* Marx 1960
- *L. signifer*
  - *s. signifer* Duméril & Bibron 1837
  - *s. annectens* Boulenger 1901
- *L. williamsi* Laurent 1991

fitzingerii group

- *L. boulengeri* Koslowsky 1898
- *L. chacoensis* Shreve 1948
- *L. darwinii* Bell 1843
- *L. donosobarrosi* Cei 1974
- *L. fitzingerii*
  - *f. fitzingerii* Duméril & Bibron 1837
  - *f. canqueli* Cei 1973
- *L. irregularis* Laurent 1986
- *L. melanops*
  - *m. melanops* Burmeister, 1888

APPENDIX. Continued.

Subgenus *Liolaemus*	Subgenus *Eulaemus*
L. lemniscatus Gravenhorst 1838	*m. xanthoviridis* Cei & Scolaro 1980
L. leopardinus	*L. ornatus* Koslowsky 1898
l. leopardinus Müller & Hellmich 1932	*L. rothi* Koslowsky 1898
l. ramonensis Müller & Hellmich 1932	*L. uspallatensis* Macola & Castro 1982
l. valdesianus Hellmich 1950	
L. lorenzmuelleri Hellmich 1950	
L. monticola	
m. monticola Müller & Hellmich 1932	
m. chillanensis Müller & Hellmich 1932	
m. villaricensis Müller & Hellmich 1932	
L. nigromaculatus Wiegmann 1834	
L. nigroviridis	
n. nigroviridis Müller & Hellmich 1932	
n. campanae Hellmich 1950	
n. minor Müller & Hellmich 1932	
n. nigroroseus Donoso-Barros 1966	
L. nitidus Wiegmann 1834	
L. paulinae Donoso-Barros 1961	
L. pictus	
p. pictus Duméril & Bibron 1837	
p. argentinus Müller & Hellmich 1939	
p. chiloeensis Müller & Hellmich 1939	
p. major Boulenger 1885	
p. talcanensis Urbana & Zungia 1977	
L. platei Werner 1898	
L. robertmertensi Hellmich 1964	
L. sanjuanensis Cei 1982	
L. schroederi Müller & Hellmich 1938	
L. tacnae Shreve 1941	
L. tenuis	
t. tenuis Duméril & Bibron 1837	
t. punctatissimus Müller & Hellmich 1933	

APPENDIX. Continued.

Subgenus *Liolaemus*	Subgenus *Eulaemus*
L. variegatus Laurent 1984	
L. velosoi Ortiz 1987	
L. walkeri Shreve 1938	
L. zapallarensis	
z. zapallarensis Müller & Hellmich 1933	
z. ater Müller & Hellmich 1933	
z. sieversi Donoso-Barros 1954	

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NEW OR PROBLEMATIC *ANOLIS* FROM COLOMBIA. VII. *ANOLIS LAMARI,* A NEW ANOLE FROM THE CORDILLERA ORIENTAL OF COLOMBIA, WITH A DISCUSSION OF *TIGRINUS* AND *PUNCTATUS* SPECIES GROUP BOUNDARIES

Ernest E. Williams[1]

Abstract. A new species, *Anolis lamari,* is described from the eastern slopes of the Cordillera Oriental of Colombia. It is compared with the species previously assigned to the *tigrinus* group. The characters separating the *tigrinus* and *punctatus* species groups are reassessed. A plea is made for the temporary use of informal groupings—recognized as such—whenever sufficient grounds for the recognition of formal taxa do not exist.

INTRODUCTION

A small anole from the eastern slopes of the Cordillera Oriental of Colombia is recognized as another new species apparently allied to the *tigrinus* species group. It is named *Anolis lamari* after its discoverer, W. W. Lamar.

DESCRIPTION

Anolis lamari, new species

Figures 1–4

Holotype. ICN 6762 (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá) (formerly WWL 1576).

Type Locality. Portachuelo, about 2 miles (by air) north of Manzanares, a police inspection station in the Municipio de Aca-

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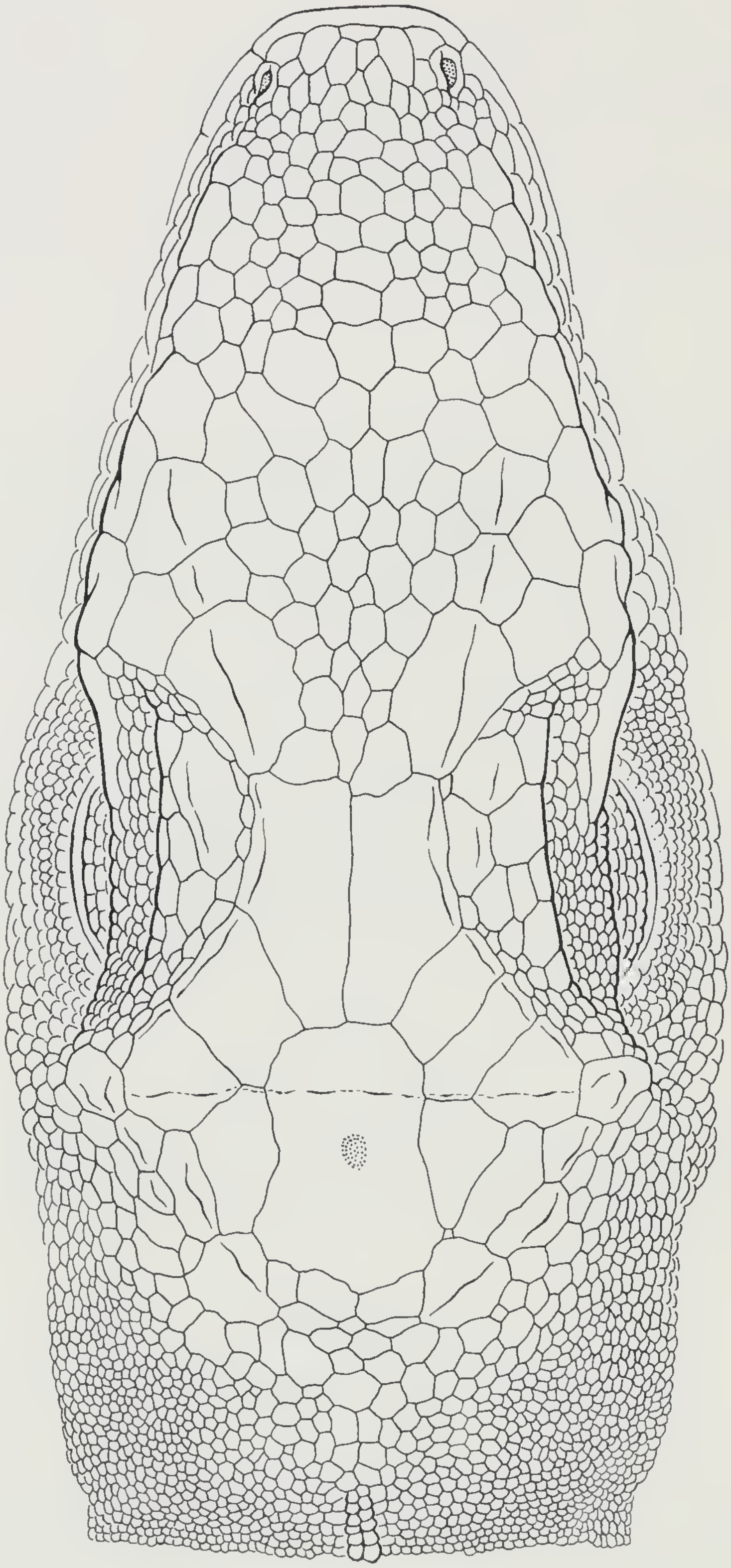

Figure 1. *Anolis lamari,* holotype. Dorsal view of head.

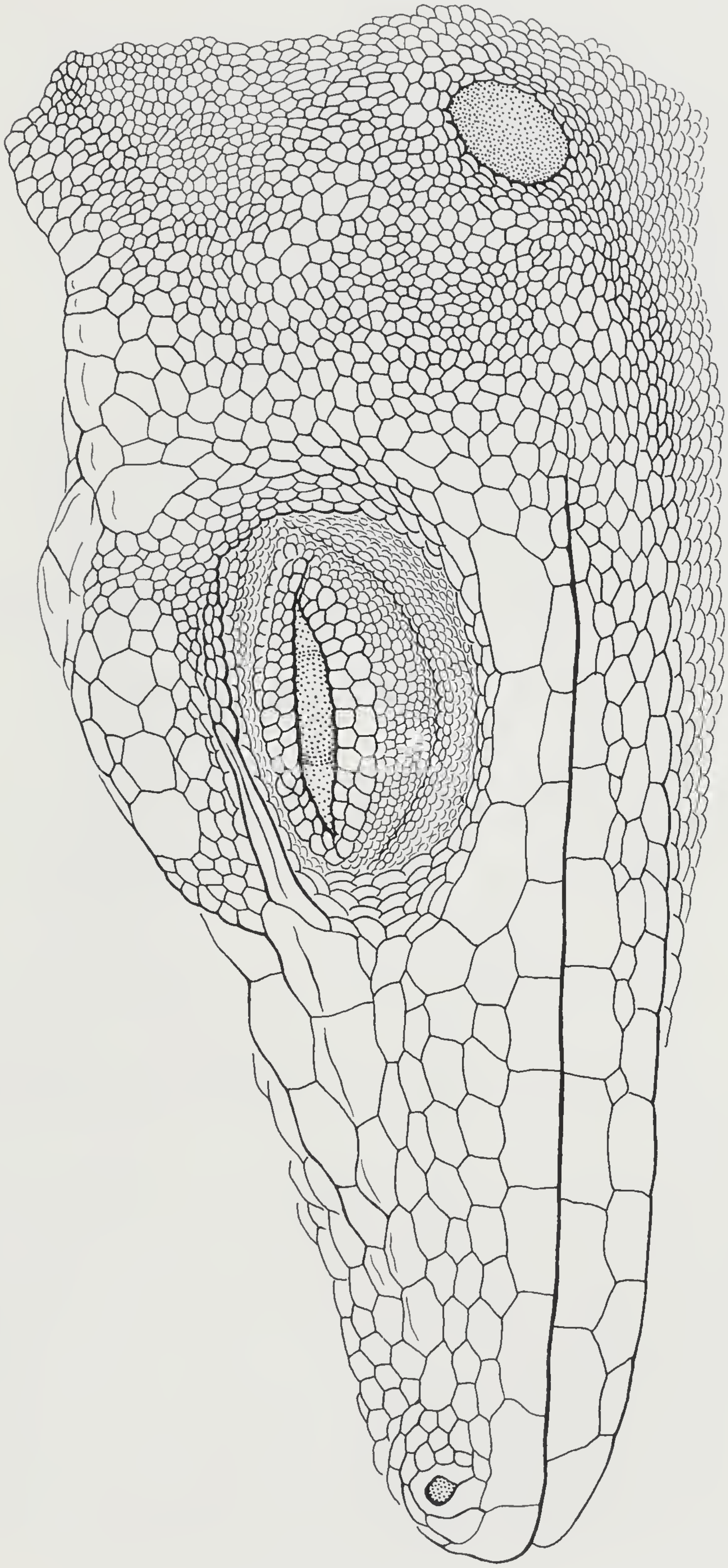

Figure 2. *Anolis lamari,* holotype. Lateral view of head.

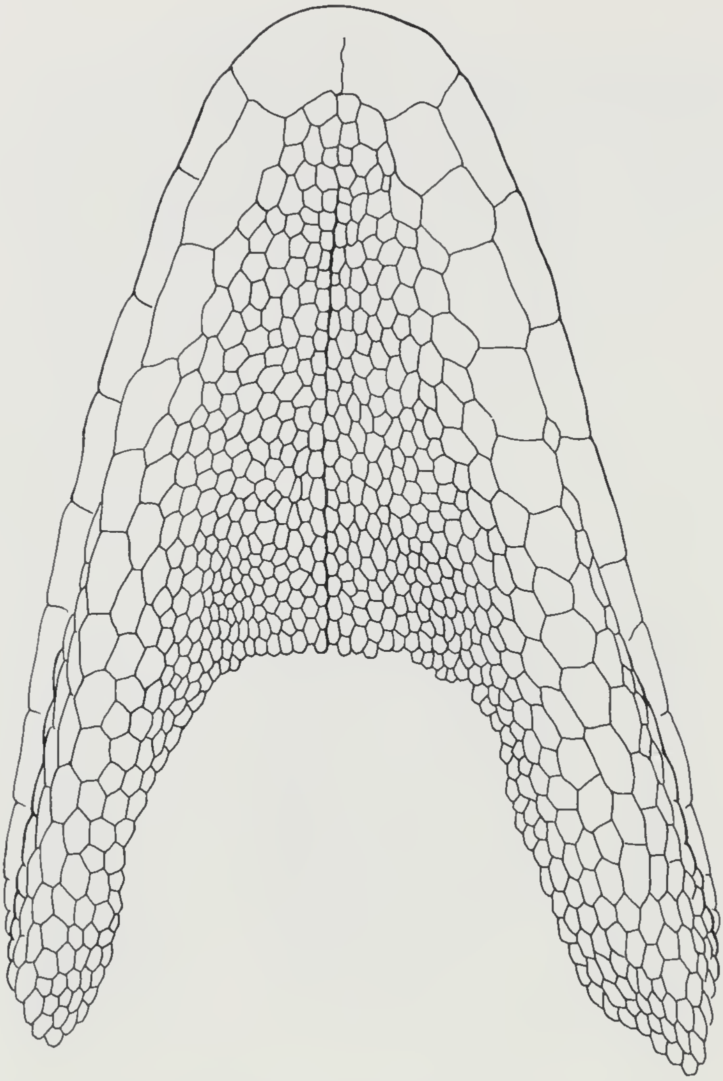

Figure 3. *Anolis lamari,* holotype. Ventral view of head.

cías, Meta, Colombia. W. W. Lamar coll. July 10, 1980. Elevation ca. 1,600 m.

Diagnosis. Close to *Anolis solitarius, tigrinus, menta,* and *ruizi,* apparently differing from all in details of coloration. It differs from *tigrinus* in the absence of minute tubercles on the head scales, from *menta* in that the dewlap is uniform yellow-orange rather than bicolor white and lemon-yellow, from *ruizi* in the possession of a small knob at the posterior edge of the parietal, and from *solitarius* in body pattern and in the presence of a line of enlarged scales continuing back onto the parietal knob. The pattern of the only known specimen, a male, is closest to that of male *ruizi,* but lacks the distinctly reticulate flanks of that species.

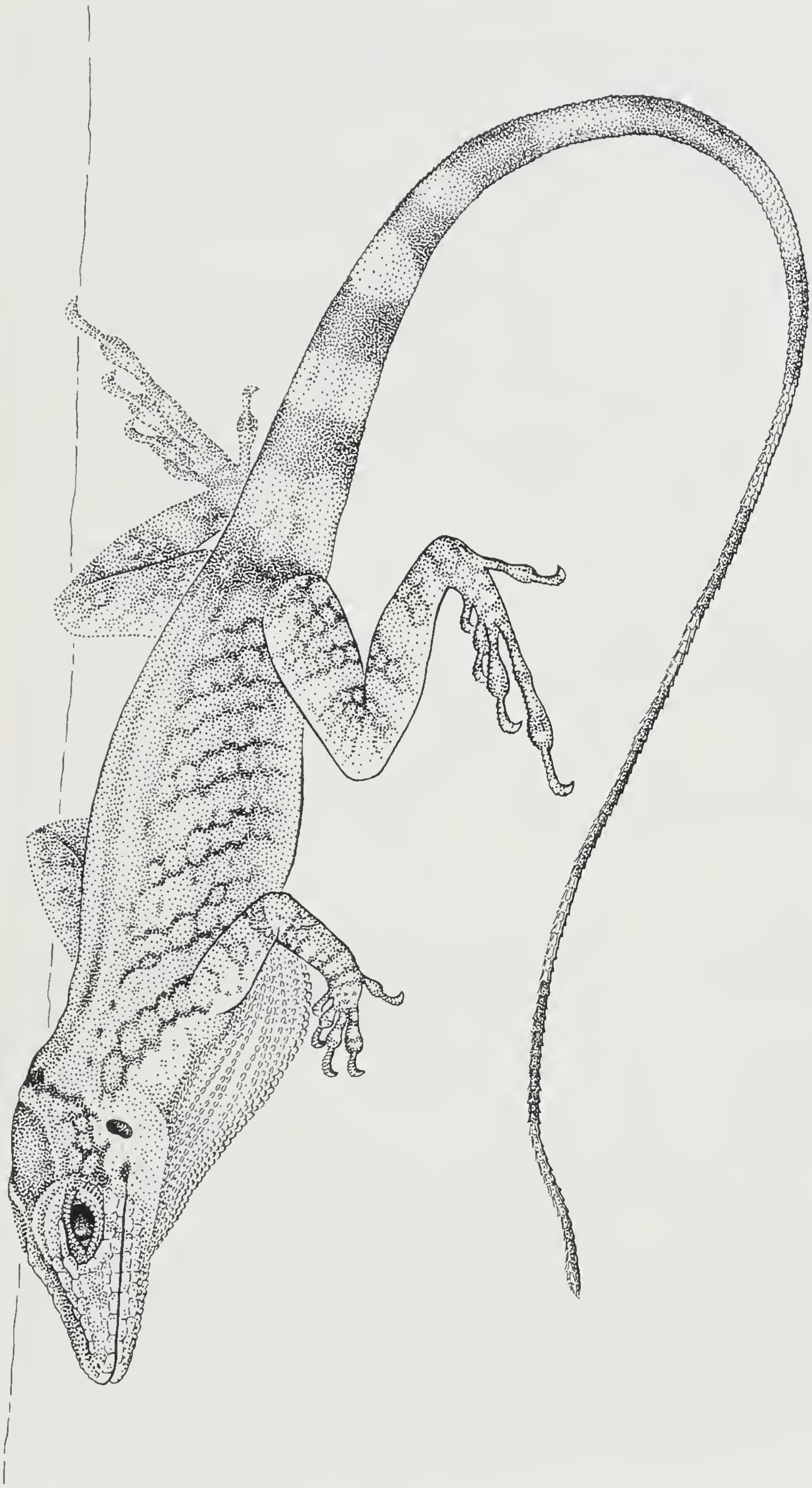

Figure 4. *Anolis lamari*, holotype. Lateral view to show pattern.

Description. Head: Dorsal head scales smooth, small anteriorly, much larger from the anterior margin of orbits posteriorly. Eight scales across snout between second canthals. The scales within the moderate frontal depression as large as or larger than those anterior to them. Five postrostrals. Large anterior nasal in contact with the suture between rostral and first supralabial. About eight scales between the circumnasals dorsally.

Scales of supraorbital semicircles very large, broadly in contact with each other and with the supraocular disks. About 16 enlarged scales in each supraocular disk, the largest medial, the disk bordered anteriorly, laterally, and posteriorly by granules. One elongate superciliary on each side, occupying about one half the lateral supraocular margin. The more posterior superciliaries minutely granular.

Canthus blunt, six canthal scales, the first and second largest becoming gradually smaller anteriorly. Three to four loreal rows, subequal; 18–22 total loreals.

Lower temporals finely granular, subequal. Two intertemporal rows on the bony bar that is the lower margin of the upper temporal vacuity. Supratemporals subgranular near the intertemporal rows, becoming abruptly larger near the interparietal. Scales just lateral to the interparietal large, ranging to one third the size of the interparietal, the latter very large, much larger than the ear, in broad contact with the semicircles. Four scale rows posterior to the interparietal relatively large but not as large as those lateral to it, and behind these a further series of four smaller scales leading to a bony boss on the parietal bone, i.e., a total series of eight scales larger than the nape scales behind the interparietal. Nape scales grading rapidly into the granular dorsals.

Suboculars in contact with the supralabials, grading anteriorly into the loreals, posteriorly becoming abruptly smaller, grading into the lower temporals. About seven supralabials to below the center of the eye.

Mental semidivided, in contact with six scales, in a gentle concave arc, between the infralabials: Four medial postmental granules and, lateral to them, a first sublabial on each side at least five times the size of the postmental granules. Behind the first sublabials on each side, three to four additional sublabials in contact with the infralabials. Medial gulars granular, convex, smooth, becoming larger near the sublabial rows.

Trunk: Dorsals smooth, juxtaposed, the two middorsal rows slightly larger, smooth or very weakly keeled. Flank scales almost as large as dorsals, smooth, juxtaposed. Ventrals much larger, subquadrate, flat, smooth, subimbricate to imbricate, in transverse rows.

Dewlap: Very large, extending posteriorly nearly to middle of belly. Edge scales smooth, imbricate, somewhat smaller than ventrals. Lateral scales narrow, in widely spaced rows separated by naked skin.

Limbs and Digits: Forelimb scales smooth, larger anteriorly, granular posteriorly. Upper thigh scales very weakly keeled, posterior thigh scales granular, lower leg scales smooth. Supradigitals of hand and foot weakly keeled. Nineteen lamellae under phalanges ii and iii of fourth toe.

Tail: Weakly compressed, scales small and smooth at base, becoming larger and keeled distally. A wider row dorsally, sometimes double, keeled. Lateral caudals smaller, weakly keeled. A midventral double row abruptly larger, sharply keeled. Postanals enlarged (male, one hemipenis extruded, bifid at tip).

Measurements. (Before preservation, provided by W. W. Lamar.) SVL 42.8 mm, total length 131 mm, dewlap 19 mm long, 8.5 mm deep.

Color. (As preserved.) Purplish to yellow-brown. Occipital area, including interparietal, dark. Snout anteriorly smudged with darker pigment. An irregular hollow triangle behind eye, narrowly bordered by black. Black oblique broken lines on nape in series with similar lines on flanks. A middorsal black line widest and most intense on the nape.

Color in Life. (Adapted from W. W. Lamar's notes.) Overall pattern complex because of scattered speckling.

Snout to eyes weak green. Lips pale creamy-tan. A bold white to gold stripe extending from below eye to ear at the level of the angle of the mouth. Distal portion of head golden tan. Body tan becoming green on posterior third. Beginning just posterior to eyes, four or five bars consisting of pairs of wavy dark green lines slanting backward and downward to venter. Middorsum with six brown rectangles all poorly defined but increasing in intensity as they approach the tail. Tail boldly banded in maroon brown and green, the brown bands fading to tan posteriorly. Limbs finely barred like sides.

Venter pinkish cream with indistinct specks, but midventer from chest to vent very pale yellow-green. Sides of belly pinkish. Vent and inner thighs and first third of tail pale yellow-green. Limbs brownish beneath, palms and soles maroon brown. Tail below banded brown and tan with some greenish cast.

The very large dewlap pale yellow-orange with pale greenish white raised scales.

Eye iris sooty-bronze, pupil narrowly ringed with gold. Eyelids translucent, tan like body.

Tongue pink.

Habitat. (From Lamar's notes.) Portachuelo is a "cuchilla de la Cordillera Oriental" of the Andes, a ridge that, at its highest point, is about 1,800 m. The area collected by Lamar was in the vicinity of 1,640 m, with the area of collection of the *Anolis* closer to 1,600 m. When collected, the unique type specimen was crawling over the mossy bank of a mountain stream on the property of Señor Chucho Cortez. The air temperature was 17.5°C. The animal was very slow-moving at that temperature but became very active when warmed up.

RELATIONSHIPS

The narrow relationships of *Anolis lamari* seem clear; its wider relationships involve some confusion.

Narrow Relationships

Apparently Corroborated Colombian-Venezuelan Relatives. A. lamari appears, on phenetic grounds, to be a close relative of the one Venezuelan and the three Colombian species with which it has been compared in the diagnosis, so close in all characters that this relationship seems corroborated. All five may then be considered geographically replacing forms within the *tigrinus* species group, as currently understood (Rueda and Williams, 1986): *tigrinus* from various localities in the coastal range of Venezuela, *solitarius* from the northern slopes of the Santa Marta Range in Colombia, *menta* from the southwestern slopes of the same range, *ruizi* from the eastern slopes of the Cordillera Oriental in the Departments of Boyaca and Casanare, and *lamari,* also from the eastern slopes of the Cordillera Oriental, but in the Department of Meta. All members of this northwestern South American complex are relatively small species (maximum known size 57 mm SVL in *tigrinus*) in montane forest. All share or tend to share certain features of squamation: (1) a large interparietal, (2) bordered laterally by large scales, and (3) usually in contact with the supraorbital semicircles, which (4) are almost always in contact, (5) relatively few scales across the snout between the second canthals (four–ten), (6) relatively few scales in the supraocular disk (11 or less, except in *lamari* [16]), (7) usually, a series (five or more) of relatively large scales between the interparietal and the nape scales, which are granular like the dorsals, (8) suboculars in contact with the supralabials, (9) large well-differentiated sublabials, except in two of 13 *tigrinus,* (10) dorsal scales uniform in size, (11) smooth ventrals larger than the dorsals, (12) lamellae under phalanges ii and iii of the fourth toe no fewer than 16 nor more than 22.

A further external feature unites *lamari* with *tigrinus, solitarius,* and *menta*: a small parietal knob coincident with the border between post-interparietal scales and the nape scales. A skeleton recently made of *Anolis solitarius* (ICN 6153) shows that the external parietal knob is, as expected, underlain by a bony spur on the parietal bone (Fig. 5). This feature is absent in *A. ruizi.*

Within this complex, differences are not sharp. Color, including dewlap color, is important. The problems within the *tigrinus* group,

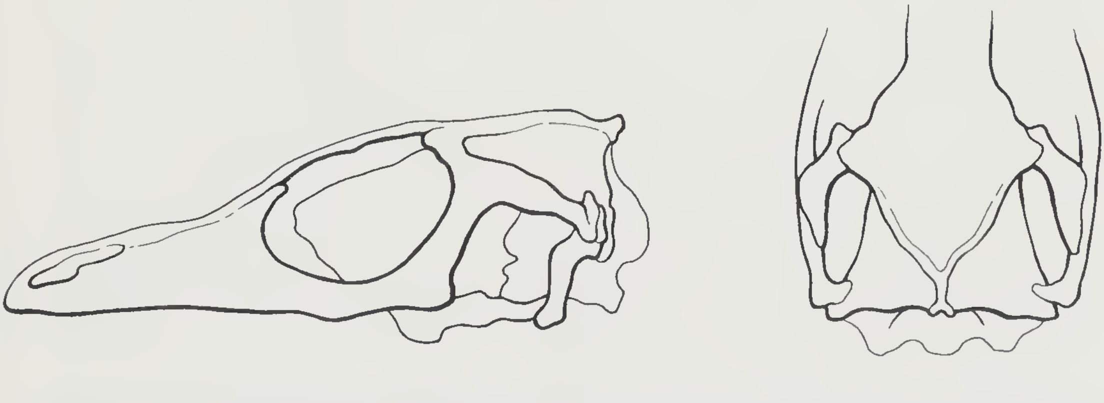

Figure 5. *A. solitarius* (ICN 6153). Left: The skull in profile. Right: The parietal bone to show the "parietal knob" and associated ridging.

as presently understood, are problems of the delimitation of taxa, not of features that unite them. It is, furthermore, not clear that all the populations referable to the group are yet known. Three of the five species, *menta, ruizi,* and *lamari,* have only recently been discovered, and no contact zones are known. The closest approach is that of *menta* and *solitarius,* which are less than 30 km apart in the west and north respectively of the Sierra de Santa Marta. *A. lamari* is the southernmost described Colombian species, but a single unnamed specimen is known from Vista Hermosa in the Sierra de Macarena that is, with high probability, the veritable southernmost Colombian record for the species group.

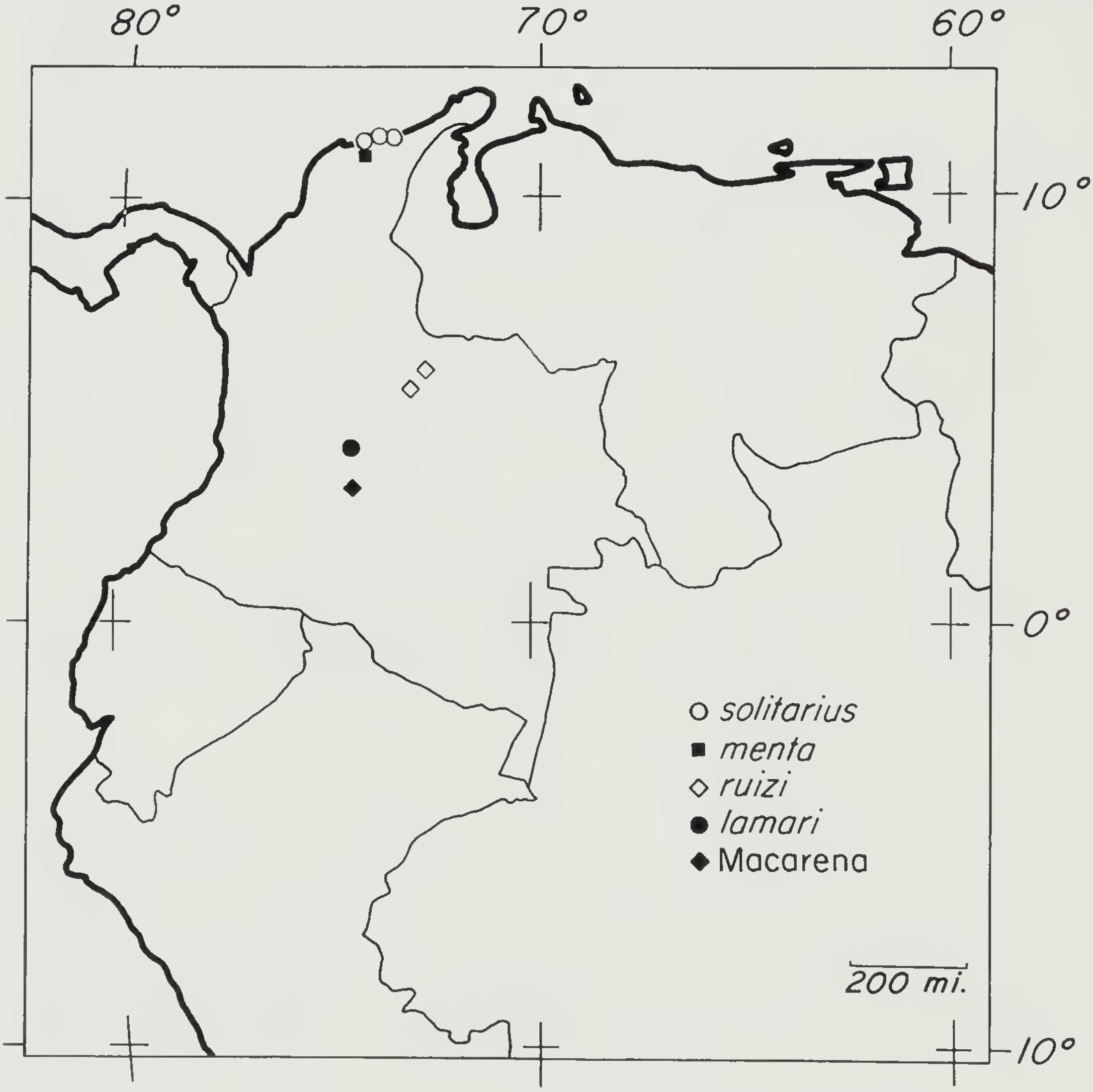

Figure 6. Colombian distribution of the *tigrinus* superspecies. MACARENA marks the presumed locality of an undescribed member of the *tigrinus* superspecies.

The locality has previously been regarded as doubtful, because it was thought to be too distant from the other Colombian species of the *tigrinus* group. No details of collection nor description of colors in life exist. (The distribution of Colombian species of this complex is shown in Fig. 6; *A. tigrinus,* as mentioned, is widely distributed in the coastal range of Venezuela.)

Of this northwestern South American complex *lamari* and *ruizi* are probably closest relatives. They are both on the eastern side of the Cordillera Oriental and show clear similarities in color and pattern (Fig. 7). They differ, however, as mentioned in the diagnosis, in the absence, in *ruizi,* of the parietal knob that is present in *lamari.*

Questionable Relationships with Two Brazilian Species. Two species, *nasofrontalis* and *pseudotigrinus,* in the Atlantic Forest

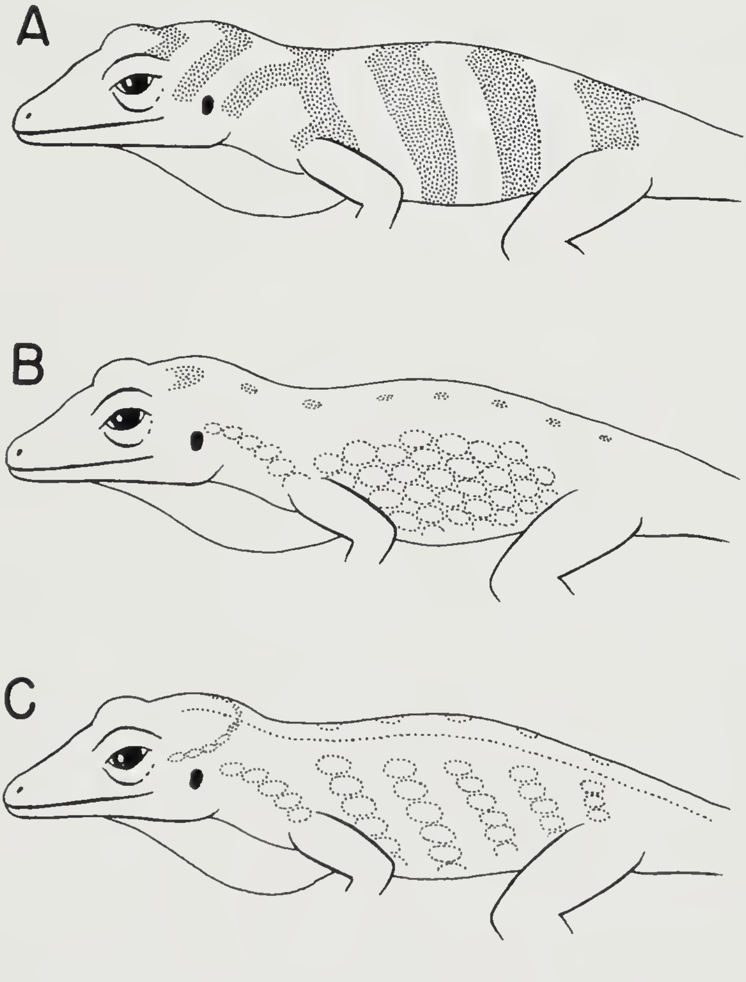

Figure 7. Male dorsal patterns in three species of the *tigrinus* superspecies. A. *A. solitarius.* B. *A. ruizi.* C. *A. lamari.*

in the state of Espirito Santo in Brazil, thus as widely disjunct from the Colombian-Venezuelan complex as the width of the South American continent permits, have been tentatively referred to the *tigrinus* species group. On size (*nasofrontalis* reaches 59 mm SVL, *pseudotigrinus* 54 mm SVL) and all scale characters they do so belong. If these two Brazilian species do belong to the same species group as the Colombian-Venezuelan complex, then, most probably, this is an old group. Relict populations may very possibly exist elsewhere, and the evidence on the present and past distribution of the group must at present be presumed to be very incomplete.

Remoter Relationships

Problems of Distinction of the Tigrinus *Group from the* Punctatus *Species Group.* When *A. lamari* is compared with the *punctatus* species group as presently defined, a problem arises. This is typified by the confusion that occurred even during the discovery of the type specimen.

Because a somewhat atypical adult of *Anolis huilae* (assigned to the *punctatus* species group) was found very close to the locality where the *A. lamari* type specimen was found, the small animal here described was at first thought to be a juvenile of that species. There is, in fact, no similarity in color or in pattern. The new species entirely lacks the bold spotting and nape ocellus of male *huilae.* There is some general similarity in squamation; in particular the interparietal of *huilae* may often be in contact with the supraorbital semicircles. Figure 8A shows the interparietal in *huilae,* but also that there is but one row of enlarged scales behind the interparietal in *huilae,* while in the midline in *lamari* there are eight such enlarged scales in front of the nape scales.

The source of the initial confusion between *A. lamari* and *A. huilae* was, in fact, the conspicuous very large interparietal scale in contact with the supraorbital semicircles. This condition is relatively unusual in *Anolis,* perhaps never invariable, but in certain groups or species characteristic to the point of being almost or quite diagnostic. It is one of the features apparently primitive for the *Anolis roquet* series of the southern Lesser Antilles, lost only, and then only sometimes, in the two giant species, *A. griseus* and *A. richardi.* In continental South America I count 18 described

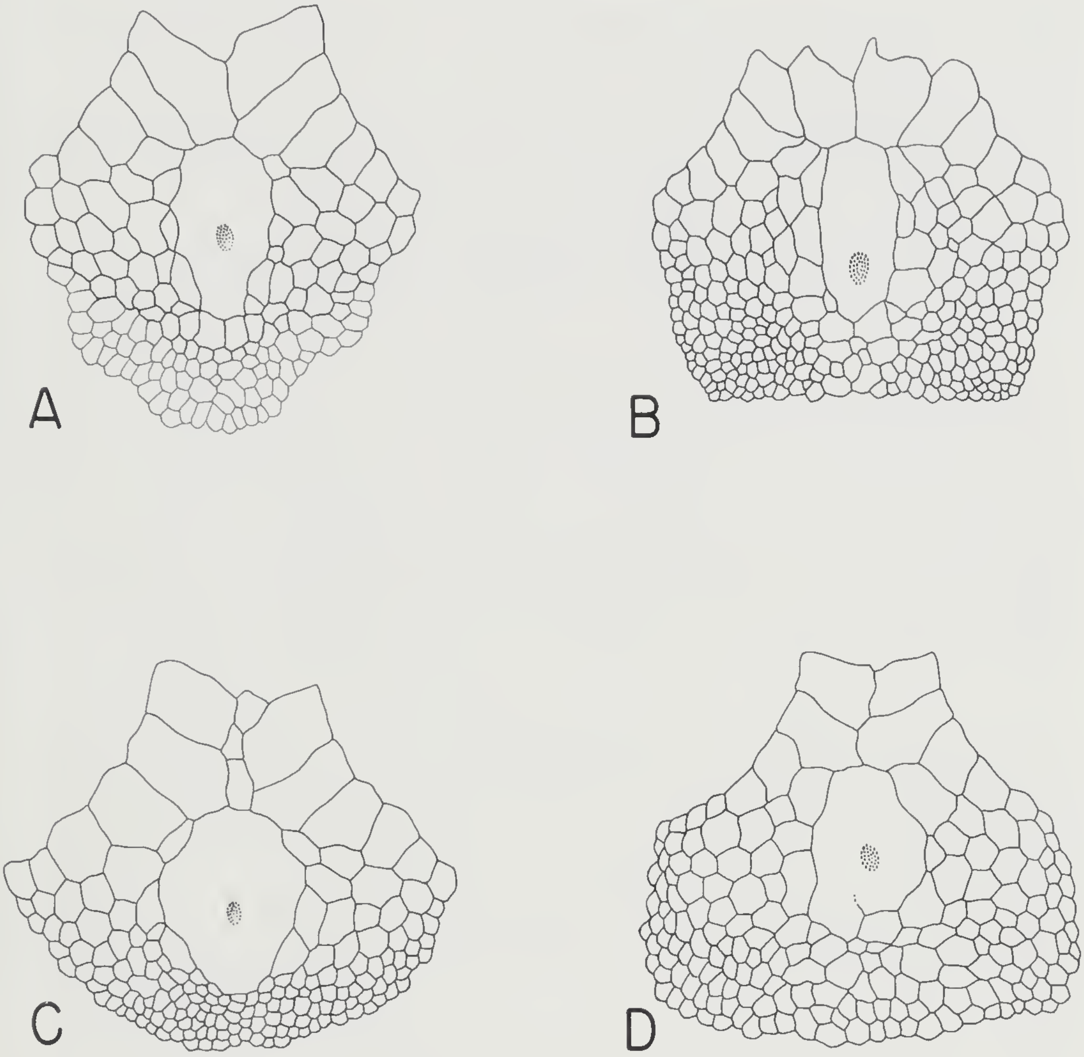

Figure 8. Scales of the parietal area in some members of the "*punctatus* species group." A. *A. huilae,* paratype: MCZ 159122. B. *A. caquetae,* holotype: MCZ 131176. C. *A. boettgeri*: MCZ 173111. D. *A. deltae,* holotype: MCNC 2031.

species of *Anolis* and three described species of *Phenacosaurus* that are known to have the interparietal in contact with the semicircles in at least some specimens. The three species of *Phenacosaurus* and five species belonging to the beta section of *Anolis, ibague, lineatus, macrolepis, rivalis,* and *meridionalis,* require no comparison with *lamari.* They and the groups to which they belong show abundant differences from the present species. Of the remainder, one, *laevis,* is known from a poorly preserved single specimen; there are not many characters to check, but *laevis* is a proboscis anole and *lamari* is clearly not.

The other species in which a large interparietal in contact with the semicircles is known are currently allocated to two species groups, the *punctatus* group and the *tigrinus* group (Williams, 1976).

In the paper just cited I provided a key in which the *punctatus* group and the *tigrinus* group were separated by couplets 5 and 6:

5. Ventrals smooth and/or dorsal squamation quite uniform 6
   Ventrals keeled, middorsals noticeably larger than flank scales 11
6. Small anoles (ca. 50 mm snout–vent length) with large flat head scales .... *tigrinus* group
   Anoles large or small but not with large head scales .... *punctatus* group

The confusion, however momentary, of *lamari,* presumed on the basis of general similarity to be a member of the *tigrinus* group, with *huilae,* assigned to the *punctatus* group anoles, demonstrates that the distinction provided by the key is inadequate. Clearly the reality of the distinction between the *punctatus* group and the *tigrinus* group needs to be better demonstrated.

The type species of the two species groups, *A. punctatus* and *A. tigrinus,* do seem to differ impressively. Three characteristics only need be mentioned: *A. punctatus* is primarily green in color, *A. tigrinus* primarily lichenate; *A. punctatus* reaches a maximum size of 89 mm SVL, *A. tigrinus* only 57 mm SVL; and in *A. punctatus* the parietal area of the head is devoid of any median prominence, in *A. tigrinus* there is posteriorly a distinct parietal knob (Ayala *et al.,* 1984). Differences of the first two sorts, color and size, however, are ecomorphic (Williams, 1972, 1983) and imply neither relationship nor lack of it. In the West Indies *A. punctatus* would fit the classic definition of a trunk-crown ecomorph, and *A. tigrinus* that of a classic twig dwarf (Williams, 1983). The character of the parietal knob is equivocal both in the South American complex that has been assigned to the *A. tigrinus* group and in the West Indies twig dwarfs: three of the West Indian twig dwarf species, *insolitus, sheplani,* and *placidus,* have such a knob; *occultus* does not; four of the South American species that are inferentially twig dwarfs have an analogous knob—*tigrinus, solitarius, menta,* and *lamari*; *ruizi* does not, and such a knob is not obvious in the two Brazilian species that have been referred to the *tigrinus* group.

Is it possible that the "*tigrinus* species group" is at best an ecomorphic (*sensu* Williams, 1972, 1983) subgroup of the *punctatus* assemblage? Even in squamation there is overlap between the two species typical for the supposed species groups. Counts across the snout between the second canthals are eight to 14 in *A. punctatus,* five to eight in *A. tigrinus.* This is confirmation that head scales tend to be smaller in *punctatus* than in *tigrinus,* but there is also overlap. Despite the difference in maximum size there is overlap in fourth toe lamellae, 22–32 under phalanges ii and iii in *A. punctatus,* 18–22 in *A. tigrinus.* While in the 11 specimens of *A. tigrinus* there is no example in which the supraorbital semicircles are not in contact medially, there are 14 examples of separation in 110 specimens examined of *A. punctatus.* In the nine specimens of *A. tigrinus* in which the interparietal can be seen, eight have the interparietal in broad contact with the semicircles; only the type of the inferred *tigrinus* synonym, *impetigosus,* has it separated by two scales. However, in none of the 110 specimens of *punctatus* is the interparietal even in point contact with the supraorbital semicircles.

And, while these two type species of the two "species groups" are on balance rather sharply distinct, the additions made to our knowledge of old species placed in the two groups and the recent referral of new species to one or the other of the two assemblages have greatly reduced the distinctiveness of one assemblage as compared with the other.

In the case of the *tigrinus* group, *solitarius* and *menta* are green rather than lichenate. A parietal knob is not visible externally in *ruizi,* nor in Brazilian *nasofrontalis* and *pseudotigrinus.* Some species currently referred to the *punctatus* group are nearly as small as members of the *tigrinus* set, and some of these are species that have or frequently have a large interparietal broadly in contact with the supraorbital semicircles: *caquetae* (maximum SVL 58 mm), *deltae* (maximum SVL 58 mm), *dissimilis* (maximum SVL 56 mm).

The one character that, on inspection of all species belonging to both species groups, appears to separate all members of the *tigrinus* grouping from all species—*except one, Anolis santamartae*—referred to the *punctatus* grouping is the enlarged scales lateral to the very large interparietal (Fig. 9). Such enlarged scales are not seen in even those species (with the exception of *santamartae*) now referred to the *punctatus* group that have a large interparietal and are similar in size to members of the *tigrinus*

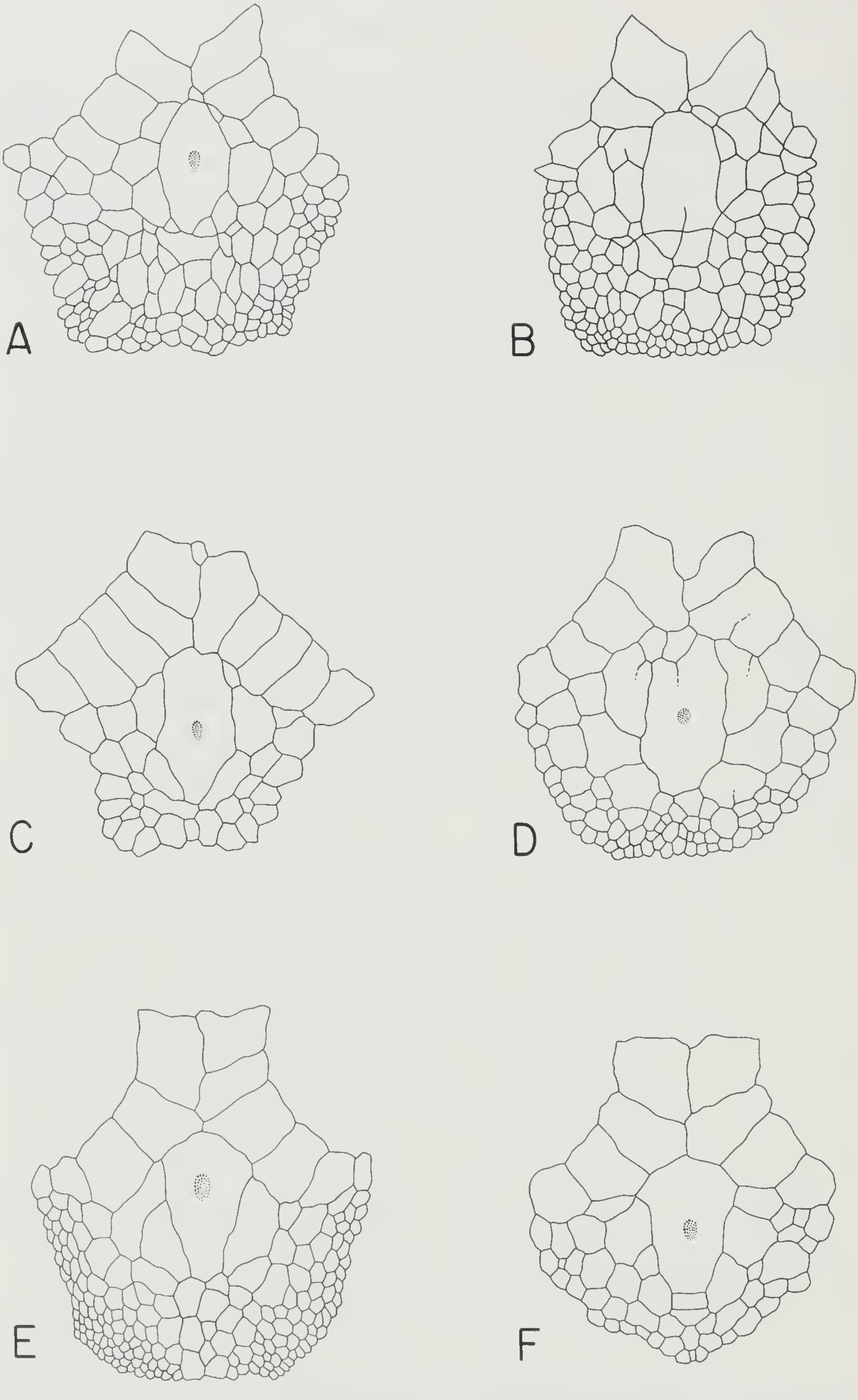

Figure 9. Scales of the parietal area in members of the "*tigrinus* species group." A. *A. nasofrontalis.* B. *A. pseudotigrinus.* C. *A. tigrinus.* D. *A. solitarius.* E. *A. menta.* F. *A. ruizi.*

group (Figs. 8, 10). (It is noteworthy that the members of the *roquet* series, which primitively show the interparietal in contact with the supraorbital semicircles, also lack these large scales lateral to the interparietal.)

A. santamartae: An Anomalous Species. The one exception within what I have called the *punctatus* species group, *Anolis santamartae* Williams, 1982 (the significant parietal area is shown in Fig. 11), is the only species of alpha anoles known to occupy the southeast corner of the Sierra de Santa Marta, the north end of which is occupied by *A. solitarius* and the southwest by *A. menta.* It might be plausible to consider *A. santamartae* on geographic grounds alone as a possible member of the *tigrinus* group.

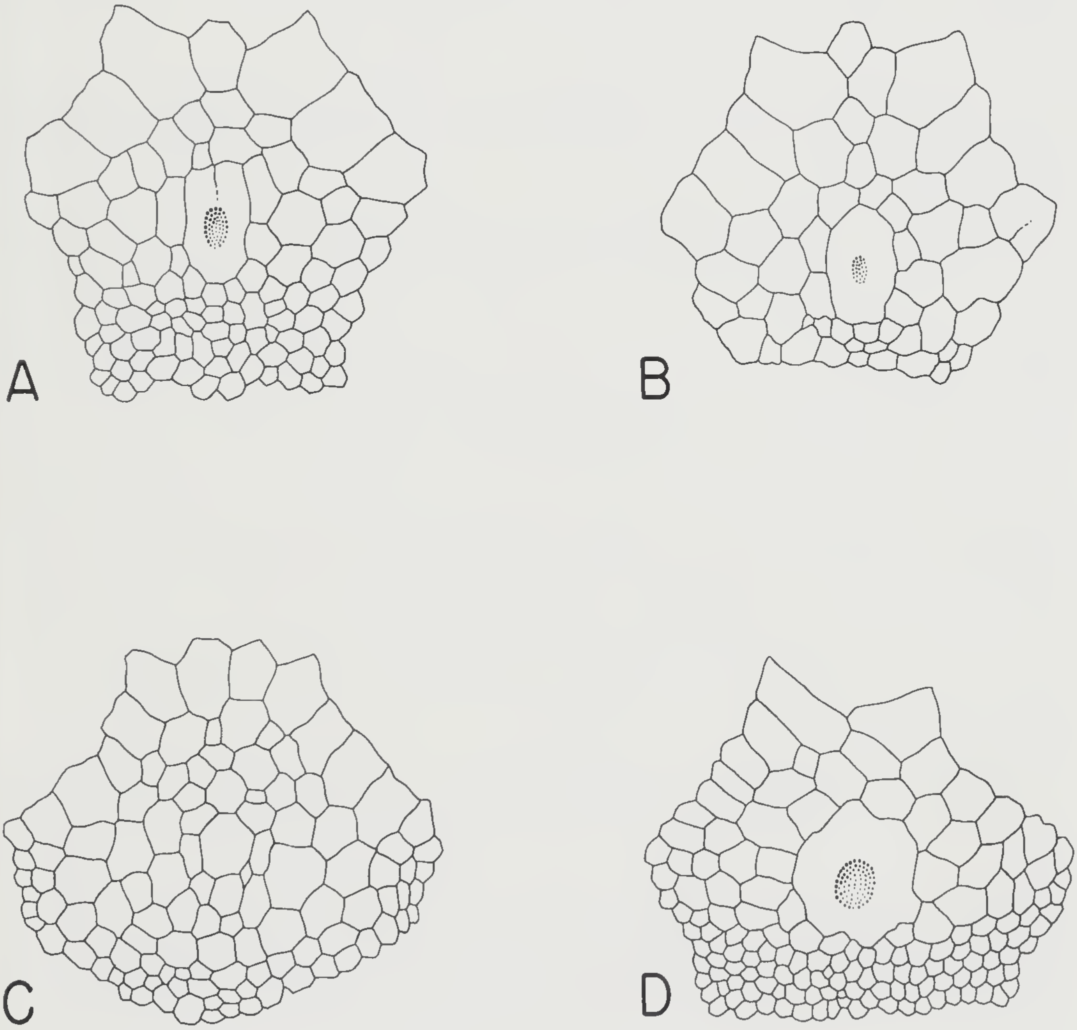

Figure 10. Scales of the parietal area in some members of the "*punctatus* species group." A. *A.* sp. ? near *transversalis*: MHNJP 1192. B. *A. jacare*: AMNH. C. *A. calimae,* holotype: MCZ 158392. D. *A. dissimilis*: FMNH 81369.

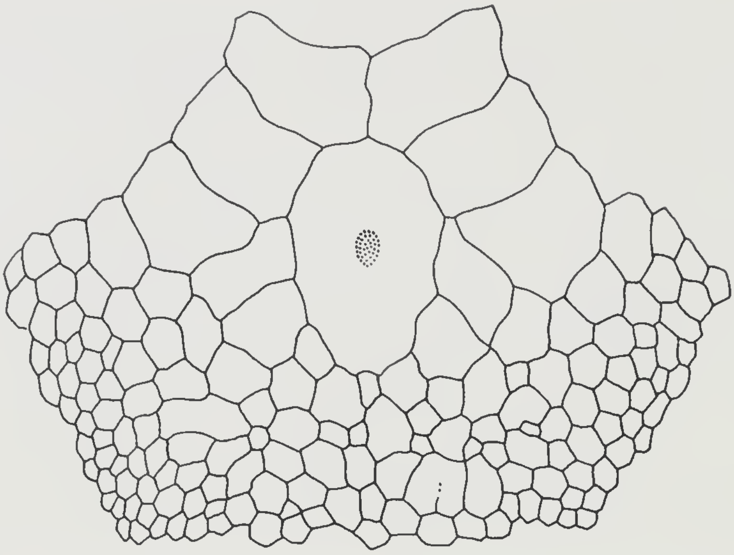

Figure 11. Scales of parietal area in *A. santamartae,* holotype: CAS 113922.

I did consider this possibility when I described it: it is the right size, approximately the right habitus. Its habits and habitat are undescribed.

Why did I reject this hypothesis? On the basis, first, of the distinctive pattern, in particular the light line from the lower jaw onto the upper arm (not emphasized in the rather muted figure of the type in the original description, but stressed in the text and very evident in one of the paratypes, MCZ 156311, the pattern of which is diagrammed in Fig. 12). This is a singular and distinctive pattern for any anole. I was much more comfortable in assigning *santamartae* to the *punctatus* species group, which I knew to be quite varied in pattern, rather than to the *tigrinus* species group, which I then believed to be rather uniform in pattern, its members differing among themselves primarily in dewlap color.

When *santamartae* was described in 1982, *menta* Ayala, Harris, and Williams, 1984, and *ruizi* Rueda and Williams, 1986, were not yet recognized. I had not yet seen the large new series of *solitarius,* collected by Pedro Ruíz and John Lynch, and I was not aware that the ground color of that species in life was green. I was confident that the *tigrinus* series was ecologically the equivalent of the twig dwarf species of the West Indies. The West Indian twig dwarf anoles are basically cryptic in pattern, lichenate, as *tigrinus* was known to be. I did not expect a relative of *tigrinus* to have the pattern of *santamartae,* even if *santamartae* did have

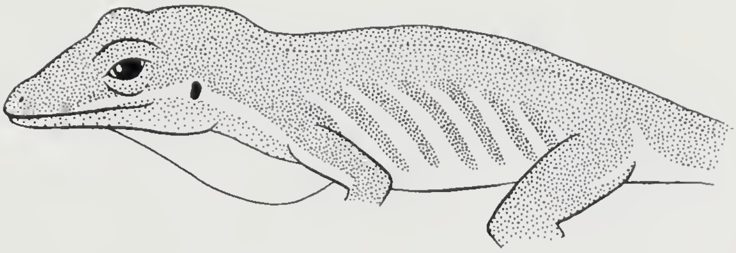

Figure 12. Male dorsal pattern in *A. santamartae,* after MCZ 156311, a paratype.

much of the size and habitus of *tigrinus.* Unhappily, the extrapolations as regards pattern from the West Indian twig dwarf ecomorphs have proved quite wrong. Additionally, the distinctly, although rather weakly keeled, dorsals and ventrals influenced me. Keeled ventrals are unusual even in the *punctatus* species group, but they are known in *punctatus* itself. The *boulengeri* morph of that species, characteristic in western populations, has keeled ventrals. There was no indication of comparable conditions in the known species of the *tigrinus* species group. There is also no evident parietal knob in *santamartae.* If *santamartae* belongs to the *tigrinus* species group, it is the most distinctive of the included species.

Remaining Problems in the Recognition of the Tigrinus *Group.* Even if the *tigrinus* group is phenetically recognizable, is it phylogenetically a unit? There are several difficulties here. One is the possibility, mentioned above, that the *tigrinus* group is an ecomorphic grouping: The *tigrinus* group may be the South American twig dwarfs. On the limited present evidence they seem likely to be so in an ecological sense. However, the scale character, the enlarged scales lateral to the parietal, by which the group may possibly be recognized morphologically, is not an attribute of twig dwarfs as an ecomorphic category. It is not present in any of the classic West Indian twig dwarfs. This possibility may provisionally be dismissed.

Unfortunately another possibility cannot be so readily dismissed. The polarity of the diagnostic scale character is in doubt. One of the two possibilities in the analysis of head scale characters in the Squamata is that small undifferentiated head scales are primitive, and that they have repeatedly united in larger units. The other is that large scales like parietals, frontals, postparietals, etc., are primitive. In the first hypothesis the larger scales lateral

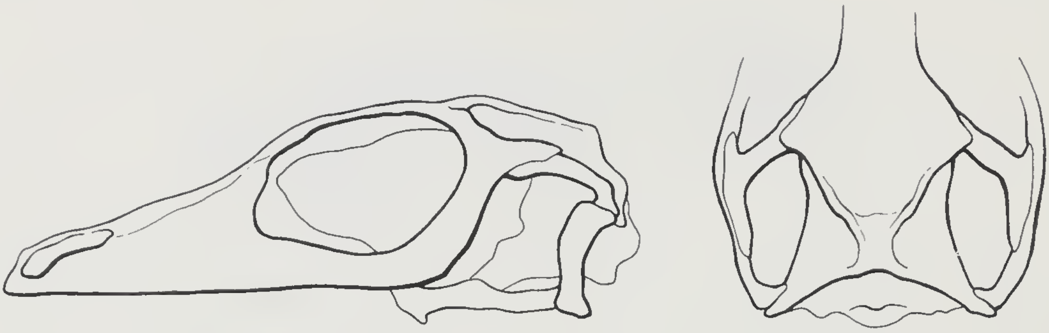

Figure 13. *A. punctatus* (MCZ 155994). Left: The skull in profile. Right: The parietal bone to show absence of the parietal knob.

to the interparietal are genuinely synapomorphic, and the *tigrinus* group is a genuinely monophyletic unit that includes the two widely disjunct Brazilian species. In the second hypothesis, which I favor on general grounds rather than the specifics of this case, the larger scales lateral to the interparietal are remnants of primitively present parietal scales in this area. Then, the *tigrinus* group may not be monophyletic, but merely an assemblage of possibly only remotely related species that happen to remain plesiomorphic in the size of the scales lateral to the interparietal. The Colombian set of species might be genuinely a superspecies, but the Brazilian members of the assemblage would be only species that by a combination of ecomorphology and symplesiomorphy have come to resemble their relatively distant relatives on the other side of the continent.

The parietal knob seen in *tigrinus, solitarius, menta,* and now in *lamari* seems certainly a derived character. Figure 5 shows the bony structure underlying the external parietal knob in *A. solitarius.* Figure 13 shows the complete absence of such a structure in *A. punctatus.* An approach to the *solitarius* condition is seen in *A. jacare* (Fig. 14), and in no other of the South American alpha anoles examined (*punctatus, agassizi, chloris, peraccae, gemmosus, ventrimaculatus, aequatorialis, princeps, squamulatus, latifrons,* and *frenatus*).

Etheridge in his thesis (1960) discussed the ontogenetic and phylogenetic history of parietal crests in *Anolis.* He was able to show that in the ontogeny of *Anolis carolinensis* (well illustrated in his fig. 9) the parietal crests first delimit a distinctly trapezoidal area, then a triangular area, and finally have a Y shape with the

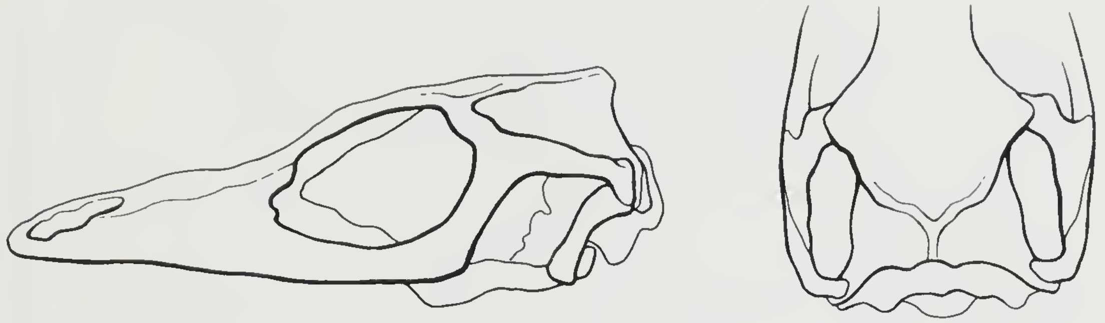

Figure 14. *A. jacare* (MCZ 112096). Left: The skull in profile. Right: The parietal bone to show similarity to *A. solitarius* in the incipient or convergent crest structure of the parietal in this species.

arms bounding the triangular area continued backward as a median ridge. He asserted that this ontogenetic sequence was precisely parallel to the sequence seen in phylogeny: *A. carolinensis,* a relatively derived species on other characters, had the Y crests in adults, whereas the South and Central American alpha anoles and the southern Lesser Antilles anoles, which are primitive in a number of other osteological characters, retain a trapezoidal crest pattern. My own observations confirm Etheridge's statements with minor revisions. Derived anoles definitely have Y-shaped parietal crests with a relatively long and narrow median posterior ridge. However, in relatively basal anoles the crests bound a trapezoidal area consistently only in the *roquet* series of the southern Lesser Antilles. In this set of species the lateral ridges do turn inward posteriorly to provide a raised transverse boundary to the parietal roof (called the occipital crest by Etheridge). However, in the primitive mainland alphas (e.g., *A. punctatus,* Fig. 13) the Y stem frequently is broad and short, a condition transitional to the fully derived Y shape. The parietal roof anterior to this posterior ridge is still trapezoidal, but lacks the distinct posterior boundary of an occipital crest that is present in the ontogenetically and phylogenetically primitive condition. *A. jacare* (Fig. 14) is still more derived. The stem of the Y is narrow—a single ridge, differing from the more advanced condition only in being short. *A. solitarius* (Fig. 5) retains the short narrow single ridge of *A. jacare,* but adds a small bony knob at the end of it, the skeletal underpinning of the external parietal knob.

The similar bony parietal knob according to this analysis occurs in some of the dwarf West Indian species (Williams, *in* Ayala *et*

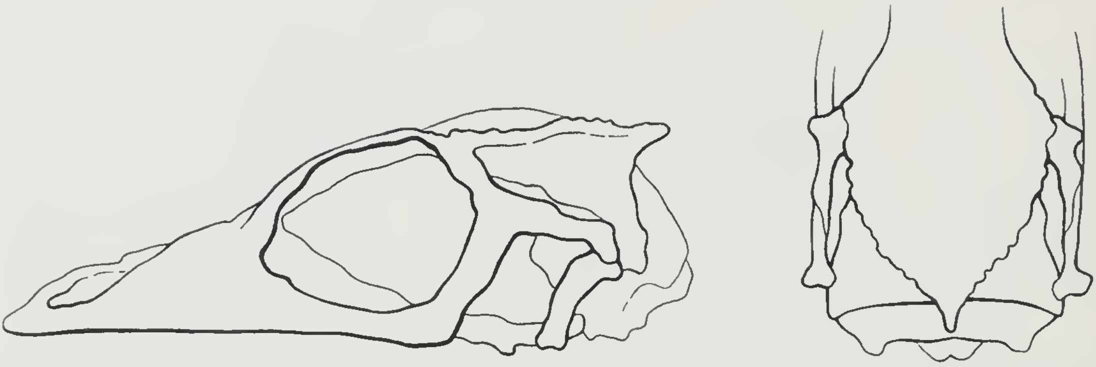

Figure 15. *A. insolitus* (MCZ 107018). Left: The skull in profile. Right: The parietal bone to show a parietal knob convergent with that of *A. solitarius.*

al., 1984; Fig. 15 in this paper). (In *A. sheplani* and *A. placidus* the skull is not known.) In *A. insolitus,* at least, the skeletal knob is at the end of a triangular parietal; there is not even a short-stemmed Y. Clearly this condition is convergent and not relevant to the issue of the monophyly of the *tigrinus* species group.

The parietal knob, defined as the condition seen in *solitarius,* might then be a synapomorphy of the *tigrinus* species group, *but* only *if* this feature has been lost in *ruizi, nasofrontalis,* and *pseudotigrinus,* as well as *santamartae, if* the latter belongs in the group. The similarity of pattern in *ruizi* and *lamari* and their geographic proximity suggest that this hypothesis of loss may be true for *ruizi.* The widely disjunct range of the two Brazilian species does not rule out this possibility for those two species, but it is clearly not as well supported. The Brazilian species were always problematic members of the *tigrinus* species group. They remain so.

CONCLUSION

I see no means to resolve the tangle presented here. I am content to speak of a *tigrinus* species group, *provided* it is recognized as a convenient means to call attention to phenetic resemblances that may or may not be phylogenetically meaningful.

As currently used, the *punctatus* group is clearly the residue of those South American alpha *Anolis* believed or known to have arrow-shaped interclavicles (Williams, 1989) that are not placed in the presumed *tigrinus* lineage. It might be a rescue of the *punctatus* group concept if the *tigrinus* lineage were placed within it. It would then consist of all South American alpha *Anolis* known or believed to have arrow-shaped interclavicles and known to have non-autotomic caudal vertebrae as adults. Even this would be a dubious rescue, again because of a question of polarity. I see no objective grounds for deciding whether arrow- or T-interclavicles, *sensu* Etheridge (1960), are primitive. This leaves me again with the *punctatus* group as a cluster of convenience, intended not to formally decide a phylogenetic question but to informally raise that question.

The problem of which the present case is an example is a pervasive and difficult one, and very clearly not limited to the genus *Anolis*. A useful recent discussion, with a summary of the pertinent literature, is that of Bauer *et al.* (1988). *I very much concur with their point that "species groups" are not formal taxa, but often, perhaps usually, operational clusters, phenetic groupings of convenience, intended at best to suggest possible affinities but not pretending at all to their demonstration.* I disagree with Bauer *et al.* in being less optimistic than they that data sufficient for the analysis that they hope for will soon be available.

I plead for extensive periods of use of informal groupings in cases in which taxonomic decisions must be based on evidence that is less than conclusive. The levels of confidence for every taxon erected or changed need not be quantified—there may be no plausible means of doing so—but the grounds for these levels of confidence should always be spelled out in detail, as I have attempted to do in this paper.

ACKNOWLEDGMENT

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A NEW *SPHAERODACTYLUS* (SAURIA: GEKKONIDAE) FROM BEQUIA, GRENADA BANK, LESSER ANTILLES

JAMES LAZELL[1]

ABSTRACT. A new species of *Sphaerodactylus* of small size (25 mm SVL) is described from Bequia, Grenada Bank, Lesser Antilles. It is without keeled scales; with large, subimbricate lateral dorsals (10–12 in standard distance at midbody) and slightly smaller, convex middorsals (12–15 in standard distance); with large, imbricate, cycloid ventrals (8 in standard distance); and with a blotchy, obsolete pattern in somber colors. Its discovery fills a long-standing biogeographical gap.

> *I believe sufficient collecting will demonstrate sphaerodactyls to be present.*
>
> Wayne King (1962)

INTRODUCTION

The small geckos of the genus *Sphaerodactylus* are nearly ubiquitous in the West Indies. They occur on tiny fragments of land less than a hectare in area (e.g., Watson Rock in the British Virgin Islands: Museum of Comparative Zoology [MCZ] 176729). There are dozens of species on some of the larger Greater Antilles (Haas, 1991). The absence of a species of *Sphaerodactylus* from the Grenada Bank, southernmost of the Lesser Antilles, has long been a sore point for biogeographers (King, 1962; Williams, 1989; Haas, 1991).

In 1964, I first went down through the Grenadines—small islands on the northern two-thirds of the Grenada Bank—collecting specimens. I travelled on the sloop *Flamingo,* a St. Vincent government fishing vessel. My trip was arranged by Dr. I. Earle Kirby, then St. Vincent government veterinarian, and always an avid naturalist. In November 1989 I returned with Thomas Sinclair, of The Conservation Agency, and Christopher Luginbuhl, of the

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David B. Luginbuhl Foundation, with the intention of exploring possibilities for a biological station on Luginbuhl's property on Bequia, Grenadines. We obtained specimens of a distinctive *Sphaerodactylus,* reported as *"Sphaerodactylus cf. vincenti"* by Lazell and Sinclair (1990). Dr. Kirby, who had spent the intervening years working to develop science, education, and conservation in St. Vincent and the Grenadines, advised us on procedures and arranged meetings and logistics that insured our success.

The contributions of Earle Kirby to progress and enlightenment in the Caribbean are legion; see Gibson, in Jinkins and Bobrow, 1985. I thus take pleasure in naming:

Sphaerodactylus kirbyi, sp. nov.

Type. MCZ 175141, adult male, collected by Thomas Sinclair, 30 November 1989. See Figure 1.

Type Locality. Slope above Friendship Bay, Bequia, Grenadines. See Figure 2.

Diagnosis. A small species (to 25 mm SVL) of moderate rather than attenuate proportions: axilla to tip of snout ca. 44 percent (40–48, av. 43.8 ± 2.9) of snout–vent length (SVL). Standard distance (STD), tip of snout to center of eye, 14–16 (av. 14.7 ± 0.8) percent of SVL. No keeled scales, but lateral dorsals at midbody convex to subtectiform, subimbricate, and large: 10–12 (av. 11.3 ± 0.8) in STD; middorsals slightly smaller, convex, 12–16 (av. 14 ± 1.7) in STD; ventrals imbricate, cycloid, and large: 8 in STD; 10–12 (av. 10.3 ± 0.8) subdigital lamellae, counting the terminal spheroid. Subcaudals at least twice the width of lateral caudals. Coloration somber, shades of gray-brown, with irregular small blotches and dim cephalic stripes.

Description of the Type. MCZ 175141 is an adult male 23.6 mm SVL. The standard distance (STD) is 3.4 mm, 14 percent of SVL. There are 11 large, convex, subtectiform, slightly imbricate, lateral dorsals contained in STD at midbody. The middorsals are rather similar, convex, juxtaposed scales, and slightly smaller: 12 contained in STD. The ventrals are large, flat, and cycloid: 8 in STD. The gulars are smooth, mostly granular, but enlarged and elongate close to the mental; counting from immediately posterior to the mental, there are 17 gulars in STD. There are 10 subdigital lamellae, counting the terminal spheroid, under the fourth toe of

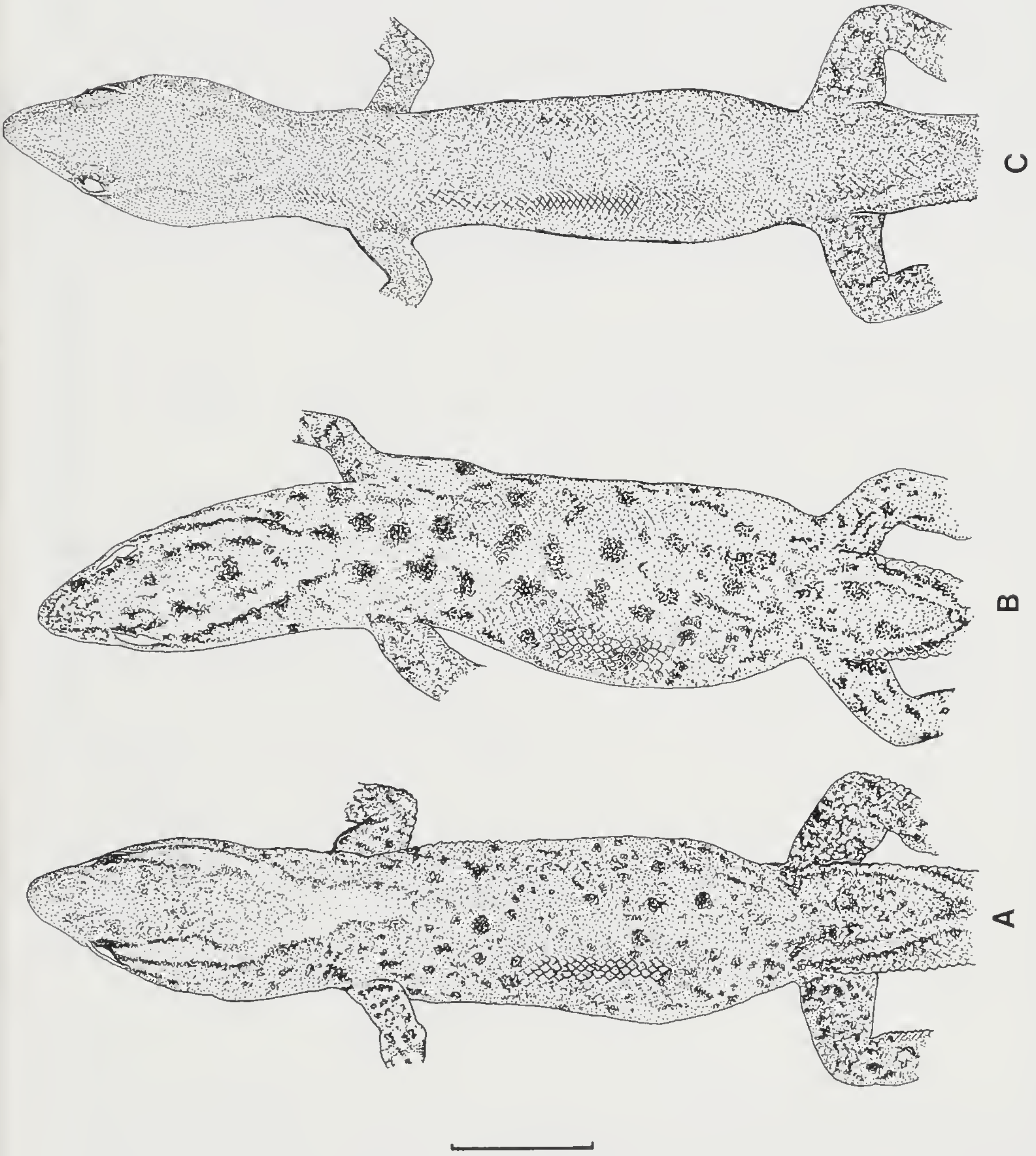

Figure 1. *Sphaerodactylus kirbyi*: A, the type, male, MCZ 175141, and B, a paratypic female, MCZ 175144. C, *Sphaerodactylus v. vincenti*, MCZ 79723, Cane Garden, St. Vincent.

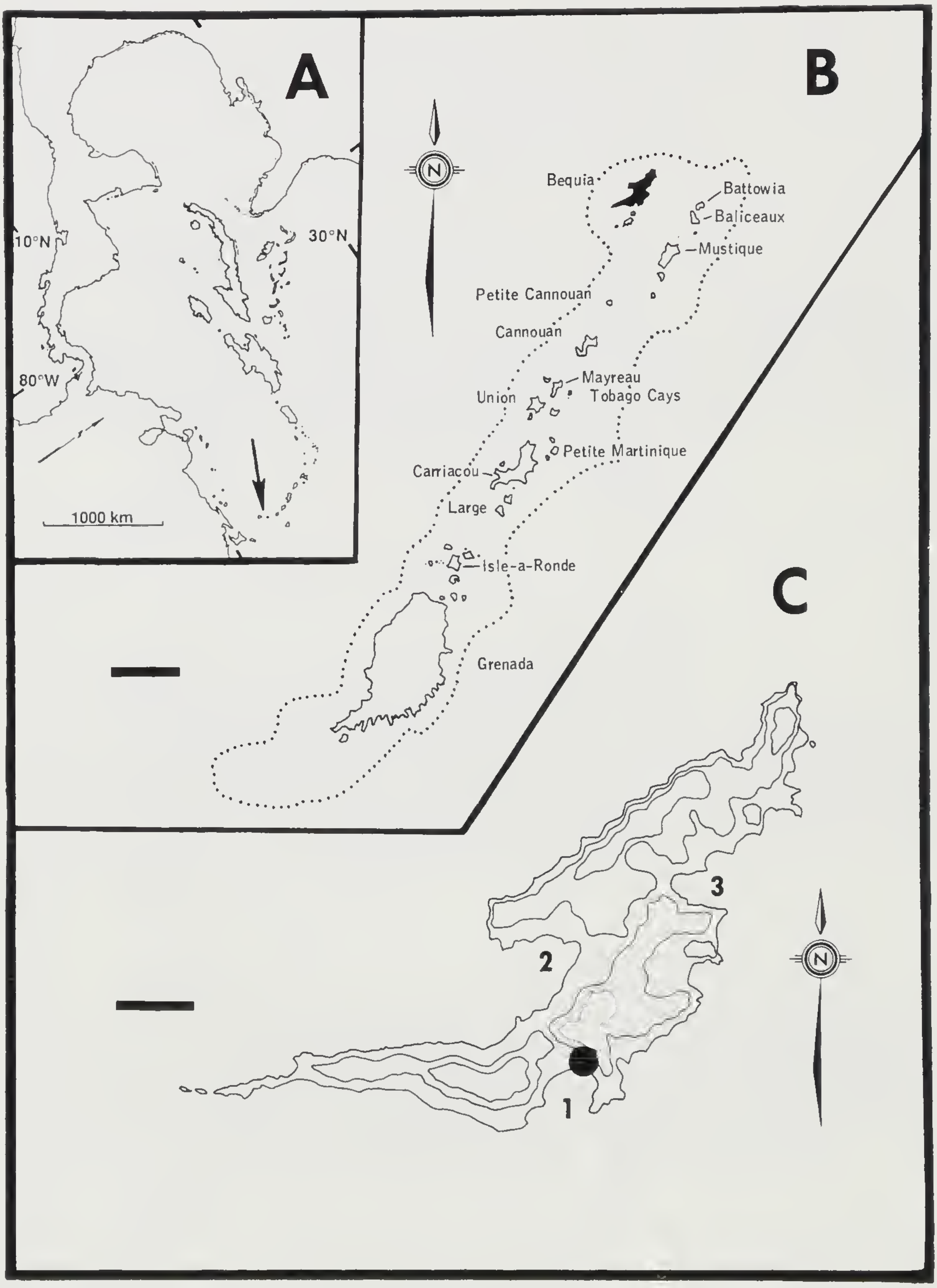
A
B
C
10°N
30°N
80°W
1000 km
Bequia
Battowia
Baliceaux
Mustique
Petite Cannouan
Cannouan
Mayreau
Tobago Cays
Union
Petite Martinique
Carriacou
Large
Isle-a-Ronde
Grenada
N
1
2
3

Figure 2. Type locality of *Sphaerodactylus kirbyi*. A, the Caribbean basin; arrow indicates the Grenada Bank. B, the major islands of the Grenada Bank. Bequia is shaded. The dotted line indicates the approximate land area of greater Grenada at glacial maximum, ca. 12,000 yr BP. Bar is 10 km. C, Bequia: contours are approximately 100 m; 1, Friendship Bay; 2, Princess Margaret (formerly Admiralty) Bay; 3, Spring Bay. Bar is 1 km. Dot indicates area in which type series was collected.

the pes. There are three large supralabials, the third subtending the eye, followed by three small, granular supralabials to the commissure of the mouth.

In contrast to the gracile, attenuate, long-necked habitus of *Sphaerodactylus v. vincenti* (and *S. molei* of Trinidad), the proportions are more ordinary by generic standards. The distance from the axilla to the tip of the snout is 44 percent of SVL.

The escutcheon consists of pale scales in contrast to those surrounding it, which are peppered with sooty gray-brown. It spans five scales along the ventral midline and extends out the thighs to a maximum width of 24 scales: The escutcheon is configured essentially as in most races of *S. vincenti;* see, for example, Schwartz (1964), figures 19 (*S. v. festus*), 21 (*S. v. adamas*), 22 (*S. v. psammius*), and 28 (*S. v. vincenti*).

In life, the type was somber, dark, shades of gray-brown. The belly was dark gray apart from the pallid escutcheon. There was a yellow wash on the chin, throat, and sides of the neck. The underside of the tail was mottled with rosy-orange. Color change was to velvety near-black. Apart from the small slate blotches (freckles in my notes), no pattern was apparent. Some pattern, however, is visible in the preserved specimen.

The pattern consists of irregular, small, dark blotches on the trunk. There is a rather faint linear head pattern consisting of a broad gray-tan band extending caudad through the eye and converging from each side to make a short middorsal area on the shoulders clear of blotches. This gray-tan band is bordered above and below by fine slate stripes. The dorsal of these begins on the upper eyelid and fades on the temple. The ventral begins on the snout and extends to the shoulder. Below this stripe is another, finer, irregular streak extending from the posterior edge of the eye to break up into speckles on the cheek.

Dark, slate-gray stripes extend caudad from the sacrum and converge to form a V on the tail base. This figure is subtended by an ash-brown band extending from above each hindlimb insertion to converge and form a short area clear of blotches on top of the tail. This band is, in turn, subtended by another slate-gray stripe which breaks up into blotches on the tail.

There is a light pattern of longitudinal ash-gray streaks on the yellowish gray throat.

Paratypes. MCZ 175142, another adult male 23 mm SVL, and MCZ 175143, a juvenile 17.5 mm SVL, were also collected by Sinclair above Friendship Bay on 30 November 1989. Two adult females, MCZ 175144, 23.7 mm SVL, MCZ 175146, 25 mm SVL, and a juvenile, MCZ 175145, 14.7 mm SVL, were collected by Sinclair above Friendship Bay on 6 December 1989.

Apart from the escutcheon of the male, MCZ 175142, which is 4 by 24 scales, there is no evidence of sexual dimorphism in meristic characters. Counts for the paratypes, with average and standard deviation for the entire series (including the type) in parentheses are as follows: Lateral dorsals in STD at midbody 10–12 (av. 11.3 ± 0.8); middorsals 12–16 (av. 14 ± 1.7); midventrals in STD 8 in all specimens; gulars in STD, counted from immediately behind the mental posteriorly at midline of throat, 15–18 (av. 15.7 ± 1.5); subdigital lamellae under fourth toe of pes, including the terminal spheroid, 10–12 (av. 10.3 ± 0.8).

In all specimens there are three large supralabials to the eye. Posterior to these are three to five much smaller, granular supralabials. In all specimens there are broad subcaudal plates, at least twice the width of the lateral caudals.

I saw and annotated the type and paratypes MCZ 175142–43 alive, on 30 November. Both paratypes showed faint cephalic and sacro-caudal patterns when alive; these are visible in the type after preservation. Otherwise both were very similar to the type in colors except that the smaller, MCZ 175143, had cream-color subcaudal blotches and the other adult male, MCZ 175142, had orange-brown subcaudal blotches; it is intermediate in size between the smaller and MCZ 175141, the type.

I did not see MCZ 175144–46 alive, but they are similar in coloration and pattern to the others as preserved; coloration and pattern seem little affected by preservation. The pattern elements vary in clarity and development. The male MCZ 175142 is very similar to the type, but the throat streaking is virtually absent and the throat color was cream and faintest ash-gray. The cephalic pattern breaks up into blotches on the jowls. In the juvenile MCZ 175143 longitudinal throat streaks are well developed but the color was even more somber, with no yellowish throat tint. This juvenile has a well-developed cephalic pattern, and throat with streaking as in the type, but has broad, dark sacro-caudal stripes reducing the light V on the tail base. The two females set extremes of variation. One, MCZ 175144, is the palest individual seen; preserved, the ground color is tan-brown to ash-gray. The blotches and the cephalic pattern are especially bold, but the sacro-caudal figure is irregular and weakly demarcated (Fig. 1).

The female MCZ 175146 is the darkest specimen seen. The blotching is heavy and amalgamates to marbling. Both cephalic and sacro-caudal patterns are largely obliterated by blotch amalgamation. Throat streaking is especially dark and prominent in this specimen.

Comparisons. Sphaerodactylus kirbyi resembles its closest geographic neighbor, *S. v. vincenti* of St. Vincent. St. Vincent lies a mere 8 km to the north of Bequia. However, the differences in the geckos are striking. The Vincentian form is larger, has a longer neck and more gracile proportions, and is absolutely distinct in smaller scale size and rich cephalic coloration.

I have examined 21 specimens of *Sphaerodactylus v. vincenti* from St. Vincent: MCZ 10788, the type, no precise locality; MCZ 20550, Grand Sable Estate; MCZ 38190–94 plus one untagged juvenile, Diamond Beach; MCZ 79716–19, Brighton; MCZ 79720–28, Cane Garden; MCZ 96032, Colonarie. Of these, five were examined meticulously for all measurable and meristic characters; MCZ 79720–24. Eight more were checked for both of the dorsal scale counts and midventrals in STD. I agree with King (1962) that STD counts can be skewed by allometric growth, and did not count juveniles less than 19 mm SVL. However, I believe STD counts are more useful than long counts along and around the body. The smallest *Sphaerodactylus kirbyi* seen, MCZ 175145, only 14.7 mm SVL, agrees in proportions and counts with the larger individuals. Because of its proportionately longer body, *S. kirbyi* might yield axilla-to-groin counts overlapping those of the much smaller scaled *S. v. vincenti,* but STD counts show no overlap.

In *S. v. vincenti* STD is 14–15 (av. 14.6 ± 0.5) percent of SVL, essentially identical to *S. kirbyi.* However, eight of 20 Vincentian specimens exceed 25 mm SVL; King (1962) gives the maximum length as 27 mm SVL; this fits the type specimen, MCZ 10788. *S. v. vincenti* is slender and elongate in proportions; axilla to tip of snout is relatively long, 46–53 (av. 48 ± 2.8) percent of SVL.

The sample sizes, however, are too small for statistical significance.

Scale size provides clear distinctions. In *S. v. vincenti* there are 13–15 (av. 13.8 ± 0.8) lateral dorsals at midbody in STD. There are 16–22 (av. 18.6 ± 2.4) middorsals in STD. There are 9 or 10 (av. 9.4 ± 0.5) midventrals in STD. There are 19–22 (av. 20 ± 1.4) gulars in STD counted along the midline of the throat beginning immediately posteriorly to the mental. Because of small sample sizes, I simply summed lateral dorsal and middorsal counts for the two species and obtained statistical significance (Student's *t*-test) at 95 percent level of confidence. The sum of lateral dorsals and middorsals in STD is 23–28, av. 25.3 ± 1.9 in *S. kirbyi* and 31–36, av. 32.4 ± 2.2 in *S. v. vincenti.*

Important quantitative characters are shown in Table 1.

Sphaerodactylus kirbyi resembles King's (1962) figure 12B and C of *S. v. vincenti* in pattern, but is far more spotted; the spots are larger and I refer to them as blotches (see Fig. 1). In coloration the two species are strikingly distinct. *S. v. vincenti* has a yellow head and a bluish-green iris (Schwartz, 1964:404). In my field notes of 4 and 8 June 1964, I describe individuals as "orangish on heads" with throats "orange-yellow" or "yellow," and iris "pale blue-green." *S. kirbyi* has undistinguished head coloration, with only the faintest yellowish throat tinges in some individuals; the iris is not notably colorful.

More cursory comparisons are required to *Sphaerodactylus kirbyi's* closest relative to the south, *S. molei* of Trinidad, Tobago, and the adjacent mainland of South America. I have examined 19 specimens of *S. molei.* The scales are much smaller even than in *S. v. vincenti* (King, 1962) and there are four supralabials to the eye. Like *S. kirbyi* the gulars of *S. molei* are smooth. The median subcaudals are not so large or well differentiated (illustrated by Harris, 1982:13). The sacro-caudal pattern of *S. molei* consists of subparallel, longitudinal, light, dark-bordered bands, not converging to form a sacral V as in *S. kirbyi* and *S. vincenti.* The well-developed longitudinal stripes from head to tail in *S. molei* are also distinctive.

Sphaerodactylus kirbyi has much larger scales than either *S. vincenti* or *S. molei,* which flank it north and south, respectively.

It is in no sense intermediate between these species, and cannot be argued to unify them taxonomically. Similarly, *S. kirbyi* does not fit into the elaborate pattern of geographic variation in *S. vincenti* extending from St. Vincent to Dominica. Some diagnostic and meristic characters indicative of aspects of this geographic variation are shown in Table 1.

Despite its diversity, *S. vincenti* hangs together rather well. *S. v. diamesus* of St. Lucia is comfortingly intermediate in scale size between *S. v. psammius* and *S. v. vincenti,* which flank it north and south, respectively. *S. v. psammius* of extreme southern Martinique is similarly intermediate in scale size between *diamesus* and *josephinae.* The trend to larger scales from nominate *vincenti* through *diamesus* and *psammius* to *josephinae* reaches its extreme in the isolated *S. v. adamas,* very slightly differentiated from *josephinae.*

There is something of a break across central Martinique, where sphaerodactyls are as yet undocumented. To the north occur the very large, ocellate, heavily carinate forms *pheristus, ronaldi,* and—on Dominica—*monilifer.* However, ocellate *S. v. festus* effectively bridges the gap between these forms in pattern and scale size. *S. v. pheristus* and *ronaldi* intergrade and *monilifer* seems in most respects an extension of the trend from *pheristus* to *ronaldi.* At glacial maximum sphaerodactyls like *ronaldi,* or *pheristus* × *ronaldi,* would presumably have occurred closer to Dominica than is possible today (Fig. 3). *Sphaerodactylus kirbyi* does not fit into this picture of variation in *S. vincenti* at all. In accord with my long-held views on evolutionary species (Lazell, 1972 and cited therein), I grant *kirbyi* full species status.

Relationships. S. kirbyi agrees with *S. v. ronaldi* and *S. v. monilifer* in meristics, but is utterly unlike these very large, boldly patterned, ocellate forms with heavy gular (and even chest) scale keeling. The distinctions from smaller, similarly proportioned, southern Martinique forms *josephinae* and *adamas* are weak. They have larger scales than *kirbyi* and the sum of lateral dorsals plus ventrals in STD separates them from *kirbyi,* but it is a close thing (see Table 1).

My sample sizes are so small that I had to sum the lateral-dorsal-plus-ventral counts for *josephinae* and *adamas* to dem-

Table 1. Some diagnostic characters and variation in the *Sphaerodactylus kirbyi–S. vincenti* group from the Windward Islands. Asterisks indicate those characters which best separate *S. vincenti* races from *S. kirbyi*. Presence (+), absence (−), or degree (±) of scale carination in the gular area are indicated under K; ++ indicates carination extends posteriorly onto chest or venter. All scale counts are made in the standard distance (STD), tip of snout to center of eye. MD = middorsal scales, maximum count. LD = lateral dorsal scales, minimum count. V = ventral scales at midline.

Taxon	n	K	MD	LD	MD + LD
kirbyi	6	−	12–15 (14 ± 1.7)	10–12 (11.3 ± 0.8)	23–28 (25.3 ± 1.9)
vincenti	13	+*	16–22 (18.6 ± 2.4)	13–15 (13.8 ± 0.8)	31–36 (32.4 ± 2.2)
diamesus	2	+*	16–17 (16.5 ± 0.7)	8*	24–25 (24.5 ± 0.7)
psammius	5	±*	13–15 (14.4 ± 0.9)	8–10 (9.4 ± 0.9)	21–25 (23.8 ± 1.6)
josephinae	5	±	12–14 (13.2 ± 1.1)	7–9 (7.8 ± 0.8)*	19–22 (21 ± 1.2)*
adamas	3	±	11–15 (13.3 ± 2.1)	7–8 (7.7 ± 0.6)*	19–23 (21 ± 2)
festus	2	±*	13	9–11 (10 ± 1.4)	22–24 (23 ± 1.4)
pheristus	2	++*	19–21 (20 ± 1.4)*	14–16 (15 ± 1.4)*	33–37 (35 ± 2.8)
ronaldi	2	±*	15–16 (15.7 ± 0.6)	11–12 (11.3 ± 0.6)	26–28 (27 ± 1)
monilifer	3	±±*	13	8–11 (10 ± 1.7)	21–24 (23 ± 1.7)

TABLE 1. Continued.

Taxon	MD/LD	V	LD/V	LD/V
kirbyi	1.0–1.5 (1.3 ± 0.2)	8	1.3–1.5 (1.4 ± 0.1)	18–20 (19.3 ± 0.8)
vincenti	1.1–1.6 (1.4 ± 0.2)	9–10 (9.4 ± 0.5)*	1.3–1.7 (1.5 ± 0.2)	22–24 (23.2 ± 0.8)
diamesus	2.0–2.1 (2.1 ± 0.1)*	6–7 (6.5 ± 0.7)	1.1–1.3 (1.2 ± 0.1)	14–15 (14.5 ± 0.7)*
psammius	1.3–1.7 (1.5 ± 0.2)	7–9 (8.2 ± 0.8)	1.1–1.3 (1.1 ± 0.1)	15–19 (17.6 ± 1.7)*
josephinae	1.3–2.0 (1.7 ± 0.3)	7–8 (7.2 ± 0.4)	0.8–1.3 (1.1 ± 0.2)	14–16 (15 ± 0.7)*
adamas	1.4–2.0 (1.8 ± 0.3)	7–8 (8 ± 1)	0.9–1.1 (1 ± 0.1)*	15–17 (15.7 ± 1.2)*
festus	1.2–1.4 (1.3 ± 0.1)	8	1.1–1.4 (1.3 ± 0.2)	17–19 (18 ± 1.4)
pheristus	1.3–1.4 (1.4 ± 0.1)	8–10 (9 ± 1.4)	1.4–2.0 (1.7 ± 0.4)	24
ronaldi	1.3–1.5 (1.4 ± 0.1)	8–9 (8.3 ± 0.6)	1.3–1.4 (1.4 ± 0.1)	19–21 (19.7 ± 1.2)
monilifer	1.2–1.6 (1.3 ± 0.2)	7–9 (8 ± 1)	1.1–1.4 (1.2 ± 0.2)	15–20 (18 ± 2.6)

onstrate statistical significance (despite lack of overlap) for the scale size distinction from *kirbyi* (Student's *t*-test; 95 percent level of confidence).

If a subjective assessment of overall resemblance be evidence of actual relationship, one might argue that *S. kirbyi* is more closely related to the *S. vincenti* forms of southern Martinique than to any other extant taxa. At least I cannot disprove that hypothesis with available evidence.

EVOLUTION AND BIOGEOGRAPHY

On both morphological and geographic grounds *Sphaerodactylus kirbyi* fits into the group including *S. vincenti* and *S. molei* (King, 1962). However, Haas (1991) has shown that *molei* is remote from the Antillean species biochemically. It is not surprising, therefore, that *S. kirbyi* is in no appreciable way intermediate between *vincenti* and *molei:* it does not unite these species. Within *Sphaerodactylus vincenti* there are nine forms named as subspecies. *S. kirbyi* resembles *S. molei* in lacking keeled gulars, but *S. vincenti josephinae,* from southwestern Martinique, and *S. v. adamas* from adjacent Rocher du Diamant, may also have smooth (or virtually smooth) gulars. Indeed, Schwartz (1964) argues that sphaerodactyls from this area have given rise to all the rest of the *vincenti* complex. A depiction modified from Schwartz's (1964) deployment scheme is my Figure 3A.

King (1962) presented a far simpler view, arguing that sphaerodactyls had moved up into the Lesser Antilles from an ancestral stock represented by *S. molei* today. As long as nominate *S. vincenti* from St. Vincent was the proximate form, closest in both geography and morphology to *S. molei,* this position was readily defensible. Insertion of morphologically divergent *S. kirbyi* into an intermediate geographic position immediately complicates this picture. Indeed, many of us over the years have been uncomfortable with a South American origin for southern Lesser Antillean sphaerodactyls (E. E. Williams, A. Schwartz, G. Mayer, all personal communication). Our feeling seems vindicated by the biochemical approach of Haas (1991).

Many might suggest a cladistic analysis would resolve at least the temporal sequence of lineage divergence in this group. This seems to me to be a superb example of just why and how cladistic

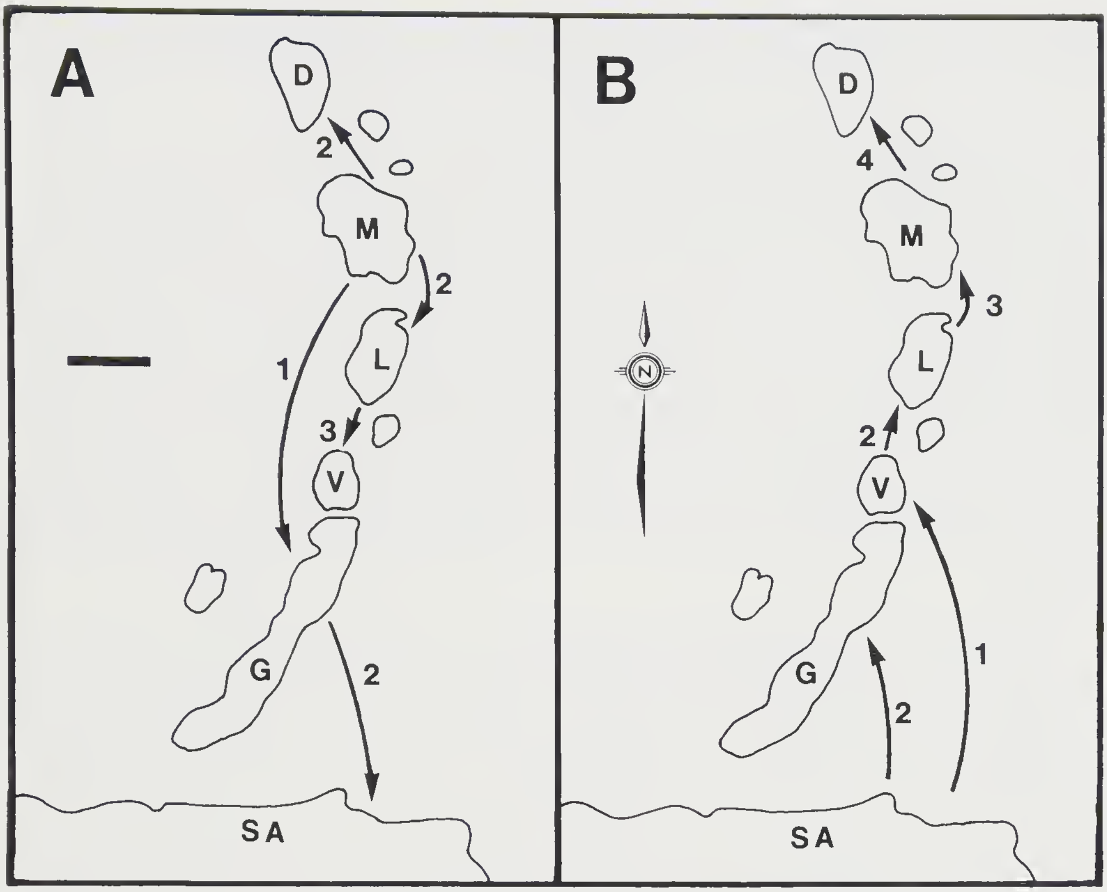

Figure 3. Scenarios for the dispersal and deployment of *Sphaerodactylus* of the *vincenti-kirbyi-molei* complex. Only the banks, which are islands at glacial maximum, and the continental shelf, mainland at glacial maximum, are shown. SA is South America. G is Grenada; V, St. Vincent; L, St. Lucia; M, Martinique; and D, Dominica. Some small banks, now submerged, but potentially important islands at glacial maximum, are shown. A is elaborated from the notions of Schwartz (1964) and B derives from the view of King (1962).

analysis fails to satisfactorily resolve relationships within the species group. There is simply no rational way of assigning polarities to the relevant characters. One may assume that small, granular dorsals are primitive in *Sphaerodactylus,* and larger granules, eventually evolving to imbricate scales, are derived. Barbour (1921) explicitly stated this and King (1962) followed suit. Accepting this notion would mean I could assume with facility that the large scales of *kirbyi* (and those southern Martinique forms of *vincenti*) are derived within the *vincenti* complex. Common sense, in combination with knowledge of habitat and of evolutionary trends in other lizards, leads me to reject this notion in this case. Large scales seem to be selected for in dry habitats (MacLean, 1985).

Thus, *kirbyi* occupies a more xeric terrain than nominate *vincenti* or *molei*. To the north, the dry country races of *S. vincenti* tend to have large scales, but the picture is not perfect.

The largest scales in any *S. vincenti* race are those of *S. v. adamas* of Rocher du Diamant, off the southwest corner of Martinique, and an arid little cay. Adjacent *S. v. josephinae,* of more mesic but still fairly dry southwestern Martinique, has scales nearly as large. However, *S. v. psammius,* of xeric Point des Salines and adjacent southeastern Martinique, and *S. v. ronaldi,* of Martinique's arid Presqu'île de la Caravelle, have significantly smaller scales. The form from northern, upland country on Martinique, originally rain forest, is *S. v. pheristus,* and it has by far the smallest scales.

Thus, among allopatric variants on Martinique we see that a very dry country form has large scales and the form from the wettest terrain has the smallest scales, but two forms from the most xeric habitats are intermediate. Gene exchange probably has retarded selection towards large scales in *S. v. psammius* and *S. v. ronaldi*—largely peninsular forms—while isolation has permitted *S. v. adamas* on its dry, steep, little islet to evolve to the extreme of large scale size for the group.

Further, *S. v. pheristus* of the erstwhile rain forest has probably been selected for small scales. In other respects such as elaborate color pattern, large size, and extreme carination, it may be the most modified ("derived") of the lot. Thus scale size cannot be assigned polarity; it is highly plastic and selected to fit specific needs in a geographically varying range.

Off Martinique, *S. v. diamesus* of the very dry northeast coast of St. Lucia has rather large scales, but they are only slightly smaller in *S. v. monilifer* from the sodden interior of Dominica. In all, the situation is suggestive of selection, but not unequivocal.

Similarly, scale carination presents no clear picture. Gular keels seem the norm for *S. vincenti,* but *S. v. josephinae* may lack them, and they may be virtually absent in *S. v. adamas.* It is facile to argue (as does Barbour, 1921, and by implication King, 1962) that keels are advanced and smooth scales primitive. Forms in genetic continuity vary—as do individuals in some panmictic populations—with respect to the presence and degree of keeling, so selection may go in either direction, and apparently has done so.

Color patterns, and even specific pattern elements, defy clear assignments of polarity. The light, dark-bordered cephalic bands amalgamating into a scapular V, and the light, dark-bordered sacro-caudal V, are characteristic of widespread, scattered, and seemingly unrelated *Sphaerodactylus.* They are present in *S. kirbyi,* nominate *S. v. vincenti,* and variably present in the other races of *vincenti.* Both pattern components are conspicuously present in such geographically and morphologically remote species as *S. macrolepis* in the Virgin Islands of the Greater Antilles, and both are quite absent from *S. molei,* which has bands that do not amalgamate to form V's.

Ocellate patterns facilitate individual recognition in dark habitats, notably in rain forest *Anolis* lizards. Ocellae are present in those *S. vincenti* from the original rain forest areas: *S. v. pheristus* of upland Martinique and *S. v. monilifer* of Dominica. In rudimentary form, ocellae are also incipient in some *S. v. vincenti* from mesic St. Vincent (King, 1962, fig. 12A). They are prominently present in *S. v. ronaldi* from arid, xeric Presqu'île de la Caravelle and in *S. macrolepis* (at least females) from the most parched islets in the Virgins, such as Watson Rock. Whether ocellae characterized the very first *Sphaerodactylus* or not is presently unknowable (but not terribly unlikely).

Sphaerodactylus kirbyi may be derived from *S. v. vincenti,* or more directly from an ancestral stock on Martinique. Of the two scenarios depicted in Figure 3, I prefer A, the one derived from Schwartz (1964). Although Haas (1991) did not have *S. vincenti* (or *S. kirbyi*) available for analysis, her evidence strengthens this view. The genus *Sphaerodactylus* seems an Antillean autochthon. Of course an aboriginal, ancestral sphaerodactyline must have first colonized the Antilles; probably the Greater Antilles. It must have departed from a continent; possibly tropical North America tens of millions of years ago, well before emergence of the Panama Land Bridge. Sphaerodactyls may have subsequently dispersed outward, over water, as waifs, to Central America, and the Lesser Antilles (Haas, 1991). Martinique, with its geologic mix of pre-Miocene to Recent igneous extrusive strata (Smith and Roobol, 1990), looks like a fine probable colonization site for the ancestral *vincenti-kirbyi* stock of *Sphaerodactylus.* It makes a good staging area for Lesser Antillean banks southward. Several other Greater Antillean stocks have demonstrably colonized the Windward Islands. *Anolis* lizards of the *bimaculatus* group, certainly of Greater Puerto Rican ancestry, have extended as far down-chain as Dominica (Lazell, 1972). *Iguana delicatissima,* whose closest relative seems to be *Iguana pinguis* of the Puerto Rico Bank (Lazell, 1989a), has colonized all the way to Martinique (Lazell, 1973). *Anolis* of the *roquet* group, a Lesser Antillean and Windward Island autochthon, have colonized some banks just off the continental shelf of South America (Lazell, 1972).

Sphaerodactylus and other Antillean forms have demonstrably colonized outward across water to mainlands. For example, ex-Antillean natural colonizers outnumber ex-continental colonizers of the Antilles at least three to two in Florida and southeastern North America. *Sphaerodactylus n. notatus* is endemic to Florida. *Crocodylus acutus* has invaded the Florida peninsula, and *Anolis carolinensis* has expanded all the way to North Carolina and Texas (Lazell, 1989b). Other species, often thought to be human introductions, may in fact involve natural colonizations: *Sphaerodactylus elegans* and the frogs *Eleutherodactylus planirostris* and *Hyla septentrionalis* are good candidates (Lazell, 1989b). The water snake *Natrix compressicauda* has gone the other way, from Florida to Cuba (Lazell, 1989b), and turtles of the genus *Chrysemys* have colonized the Greater Antilles (Williams, 1989).

At least two stocks of *Sphaerodactylus,* the species *argus* and *S. rosaurae* of the *copei* group, have colonized the Central American main or shelf islands (Harris and Kluge, 1984). Harris and Kluge (1984) say little about the origin of other Central American species. Their remark that "more than one line of evolution from the Caribbean" may be required for this modest assemblage of nine species might be taken as support for a notion of Antillean origin (as opposed to just the Caribbean coastal region of the main).

Similarly, *Anolis* lizards have colonized the Central American main: *A. mayensis* of the *sagrei* group and *A. allisoni* of the *porcatus* (or *carolinensis*) group (Williams, 1976).

My view of *Sphaerodactylus* dispersal and deployment cannot be proved or refuted on grounds of present evidence, but it sets a clear target for future work. The lines of evidence which need to be pursued are likely to be far more expensive than catching lizards and counting scales, and will certainly involve biochemistry. Haas (1991) is a firm step in the right direction, but the pattern for *S. kirbyi, S. vincenti,* and *S. molei* remains unexamined.

Sphaerodactylus kirbyi may have been derived from *S. molei* or a stock ancestral to them both. It would then retain smooth scales and have been selected in dry terrain for large scales. Its somber pattern might then be either the ancestral condition (with *molei* subsequently evolving stripes), or have resulted from selection in isolation.

Alternatively, *S. kirbyi* may have colonized the Grenada Bank, some 4,128 km^2 at glacial maximum, from southwestern Martinique. If it arrived before *S. vincenti* reached St. Vincent, then it may retain ancestral character states. Conversely, it may have arrived subsequently (in a geographic sequence that seems efficient but is quite unnecessary) and resemble the southwest Martinique forms because of a more proximate common ancestry. The strong distinctions between *S. kirbyi* and *S. v. vincenti,* its closest neighbor, are closely comparable to the distinctions in the two *Anolis* lizard species pairs which occupy these islands on separate banks (Lazell, 1972). In the cases of both *Anolis* pairs and the *Sphaerodactylus* pair, I ascribe the distinctions to adaptive selection in an arid versus a mesic habitat augmented by dichopatric character divergence resulting from failed invasions (Williams, 1969; Lazell, 1972:103).

Why has it taken so long to find sphaerodactyls on the Grenada Bank? They are genuinely scarce. I spent only about six hours hunting, and found none. Sinclair hunted about six hours each day for a week and got only six, in two sets of three, from very small areas. Sphaerodactyls are often discontinuously distributed in the Windward Islands, and sometimes appear absent from seemingly suitable habitat (the gaps on Martinique are an excellent case in point). However, *S. kirbyi* on the Grenada Bank is extreme in these respects. The presence of other chthonian and leaf-litter lizards such as *Bachia* and *Gymnophthalmus* may partially fill the *Sphaerodactylus* niche and mitigate abundance with competition.

Such a view is inevitably controversial, the more so because *Bachia* is far from ubiquitous on the Grenada Bank, known only from a few islands. *Gymnophthalmus* may be a newcomer here. Our Bequia specimens were the first recorded from the Grenada Bank (Lazell and Sinclair, 1990) and *G. underwoodi* seems to be expanding its range in the Lesser Antilles.

Our short sojourn on Bequia resulted in discovery of not just *S. kirbyi* and *G. underwoodi,* but the first *Eleutherodactylus* frog recorded for the Grenadines (Lazell and Sinclair, 1990): *E. johnstonei.* The biogeographically interesting details were lost in the editorially gutted form in which our geographic distribution notes appeared.

Since the type-locality of *Eleutherodactylus johnstonei* is on Grenada, and it is present from St. Vincent to St. Martin, virtually throughout the Lesser Antilles (Schwartz and Henderson, 1988), its occurrence on the larger Grenadines seems predictable. However, the range of this species presents numerous enigmas well described by Schwartz (1967). Briefly, there is testimony that this species was introduced to Grenada ca. 1885 from Barbados, to which it had been introduced ca. 1879. In four weeks search Schwartz himself (and Klinikowski—both superior collectors) failed to locate *Eleutherodactylus* in the Grenadines including Bequia. In five nights in the Grenadines (one on Bequia), 11–16 June 1964, I heard no frogs.

On 8 December 1989 Mr. and Mrs. Thomas Johnston, resident on Bequia, reported to Sinclair that they brought about 12 frogs from the Botanical Garden above Kingstown, St. Vincent, to Bequia in 1969. They testified that there were none on Bequia previously. These were reportedly released ca. 4 km west of Friendship Bay. Males were calling each night we were present at Friendship Bay at a density of ca. 5–6 per hectare. Despite this evidence, there is reason to doubt human introduction as the source of these populations: people catch and transport few, if any, females, and frogs, albeit native, may be cryptic for years. This species presents a singularly attractive opportunity to test molecular clocks such as mtDNA and elucidate biogeography.

The Grenada Bank, largest in the Windward Islands, is structurally and ecologically very complex, requiring comparison even to the Puerto Rico Bank of the Greater Antilles. As our efforts of a few days suggest, there is probably much left here to be discovered.

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This work is dedicated to the memory of Albert Schwartz.

We are indebted to Mr. Brian Johnson, Forestry, and Mr. Alan Cruickshank, Minister of the Interior, Government of St. Vincent and the Grenadines for permits to collect, and to Christian Luginbuhl for assistance in the field. Our trip was funded in part by the David B. Luginbuhl Foundation and The Conservation Agency.

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CHELID TURTLES OF THE AUSTRALASIAN ARCHIPELAGO: I. A NEW SPECIES OF *CHELODINA* FROM SOUTHEASTERN PAPUA NEW GUINEA

ANDERS G. J. RHODIN[1]

ABSTRACT. A new species of *Chelodina* (Testudines: Pleurodira: Chelidae) is described from the Kemp Welch River drainage basin, Central Province, southeastern Papua New Guinea, where it occurs in a restricted distribution. It is endemic to Papua New Guinea and isolated from other members of the genus. It is superficially most similar to *Chelodina novaeguineae* of southwestern Papua New Guinea, but osteologically more closely related to *C. longicollis* of eastern Australia. The recently described species *Chelodina reimanni* from southeastern Irian Jaya, Indonesia, is most closely related to *C. novaeguineae.*

INTRODUCTION

The side-necked turtles of the family Chelidae (Testudines: Pleurodira) from the New Guinean region of the Australasian Archipelago remain one of the most poorly known turtle faunas of the world. The zoogeography and the diversity of the snake-necked chelid turtle genus *Chelodina* that inhabits this region of eastern Indonesia and Papua New Guinea have received some attention, but are far from fully resolved. Until the latter part of this century only two species of *Chelodina* were known from the regions north of Australia: *Chelodina novaeguineae* Boulenger, 1888 and *Chelodina siebenrocki* Werner, 1901. *Chelodina novaeguineae* was known only from southwestern Papua New Guinea and adjacent southeastern Indonesian Irian Jaya, as well as from Roti Island west of Timor in Indonesia, with *C. siebenrocki* supposedly occurring only in "Deutsch-Neu-Guinea," the former German colony comprising the northern half of present-day Papua New Guinea. In 1976 Rhodin and Mittermeier described the

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new species *Chelodina parkeri* from the inland grass-swamps of Lake Murray and the Aramia River of southwestern Papua New Guinea. They also redescribed and clarified the distributional status of *C. siebenrocki,* which is endemic to the estuarine swamps of the southern trans-Fly region of southwestern coastal Papua New Guinea and adjacent southeastern Irian Jaya, and absent from the northern half of Papua New Guinea, where the type specimen had allegedly been collected. Subsequently, Philippen and Grossman (1990) described *Chelodina reimanni* from the coastal regions near Merauke, southeastern Irian Jaya, but did not compare their new species to the very closely related *C. novaeguineae* and provided no osteological description. Both *C. reimanni* and *C. novaeguineae* belong to the subgeneric group of *Chelodina* species that have relatively narrower heads, shorter necks, and broader plastrons designated as *Chelodina* spp. "A" (Goode, 1967; Burbidge *et al.,* 1974; Legler, 1985). Conversely, *C. parkeri* and *C. siebenrocki* are both members of the subgeneric group with relatively broader heads, longer necks, and narrower plastrons designated as *Chelodina* spp. "B".

Very little other work has appeared on the taxonomy or natural history of New Guinean and Australasian *Chelodina.* Gaffney (1977) performed a phylogenetic analysis of all Chelidae based primarily on cranial osteology and included some New Guinean taxa. Cann (1978) contributed a photographic documentary of some of the species, and Rhodin and McCord (1990) documented some reproductive parameters of *Chelodina siebenrocki.* Wells and Wellington (1985) created a host of destabilizing nomenclatorial novelties in their contentious catalogue of Australian reptiles, which has been severely criticized by the International Commission on Zoological Nomenclature (ICZN, 1991). In addition, very little research has been done on the New Guinean short-necked chelid genera *Emydura* and *Elseya.* In particular, McDowell's (1983) recent work is not generally accepted because of its sweeping synonymies (King and Burke, 1989), and Legler and Cann (1980) restricted their work to continental Australian taxa.

Over the last 20 years, I have been privileged in having access to the large Papua New Guinean chelid turtle collections obtained by Fred Parker and deposited at the Museum of Comparative Zoology by Ernest E. Williams. Early analysis of this material has led to the description of *Chelodina parkeri* and redescription of *C. siebenrocki* (Rhodin and Mittermeier, 1976). Continued study of these collections has subsequently been combined with extensive comparative analysis of specimens obtained from other museums and professional colleagues as well as from personal collecting trips to Papua New Guinea and Indonesia. To date, I have been able to examine personally approximately 700 chelid turtles from the eastern Indonesian and New Guinean regions of the Australasian Archipelago, and 450 specimens from continental Australia, for a total database of about 1,150 Australasian Chelidae. Through this study, I have reached several taxonomic conclusions regarding the chelid taxa of the Australasian Archipelago. In this, the first in a series of papers documenting these conclusions, I describe a remarkable new species of *Chelodina* from southeastern Papua New Guinea. In addition, I provide the first osteological description of *C. reimanni,* and compare both these species with *C. novaeguineae* and *C. longicollis.*

In 1985, through the courtesy of Dr. Peter C. H. Pritchard, I received two specimens of what had been assumed to be *Chelodina novaeguineae* from the vicinity of Hula, Kemp Welch River drainage, 90 km southeast of Port Moresby, southeastern coastal Papua New Guinea. These two specimens would have represented an enormous range extension for *C. novaeguineae,* which occurs primarily in the Western Province of southwestern Papua New Guinea, southeastern Irian Jaya, and northeastern Australia. The Kemp Welch population is disjunct and separated from the regular range of *C. novaeguineae* by about 500 km of relatively well-collected coastal territory including the whole developed Port Moresby region. From a preliminary examination of Pritchard's two specimens I was convinced that they represented a new and distinct species. In 1987 I traveled to Papua New Guinea's Kemp Welch River area and succeeded in obtaining a third specimen of the same taxon at Bore, Kemp Welch River. In addition, I was able to examine a fourth specimen preserved in the Papua New Guinea Museum without locality data other than "near Port Moresby". Later, through the courtesy of Dr. William P. McCord I had the fortunate opportunity to examine an additional large series of 39 live specimens obtained from just east of Bore in the Kemp Welch River area, for a total study sample of 43 animals.

These 43 Kemp Welch River specimens were then compared to a series of 51 *C. novaeguineae* from southwestern Papua New Guinea, 10 *C. novaeguineae* from northern Australia, 54 *C. longicollis* from eastern Australia, 12 *C. reimanni* from southeastern Irian Jaya, Indonesia, and 7 *C. steindachneri* from western Australia, for a total study series of 177 specimens. Analysis of external morphology and cranial osteology demonstrated that the isolated Kemp Welch population of *Chelodina* was an undescribed species. It is much more closely related to *C. longicollis* of Australia than it is to either New Guinean or Australian populations of *C. novaeguineae.* I now describe this new species and name it after Dr. Pritchard, who obtained the first two specimens and brought them to my attention.

TAXONOMY

Chelodina pritchardi, sp. nov.

(Figs. 1–3 and Table 1)

Holotype. MCZ 173543, alcohol-preserved sub-adult male of 129.5 carapace length, purchased from native villagers by Anders G. J. Rhodin on 14 August 1987 at Bore, Kemp Welch River, 13 km southeast of Kwikila, Central Province, Papua New Guinea (9°53′S, 147°46′E); specimen is also former AGJR-T 1259 and bears old tags RZ Field-13602 and AMNH 133079.

Paratypes. MCZ 175813 (former PCHP 1343) and AMNH 139735 (former PCHP 1342), obtained from natives by Peter C. H. Pritchard at Port Moresby in 1978, said to be from vicinity of Hula, Kemp Welch River drainage basin, 32 km south of Kwikila, Central Province, Papua New Guinea (10°06′S, 147°43′E).

Referred Specimens. PNGM 23373, collected by natives "near Port Moresby" (possibly in Kemp Welch River drainage basin), Central Province, Papua New Guinea, died in captivity at Moitaka Zoo, Port Moresby; AGJR-T 1575–1609, 1643–6, ca. 10 km east of Bore, Kemp Welch River region, Central Province, Papua New Guinea (39 specimens from Dr. William P. McCord's private live collection, photographed and measured by Rhodin, 13 of these (AGJR-T 1601–9, 1643–6) preserved in Rhodin's personal collection, others (AGJR-T 1575–1600) recorded in Rhodin's turtle database; all preserved specimens eventually to be deposited in the MCZ or other museum collections).

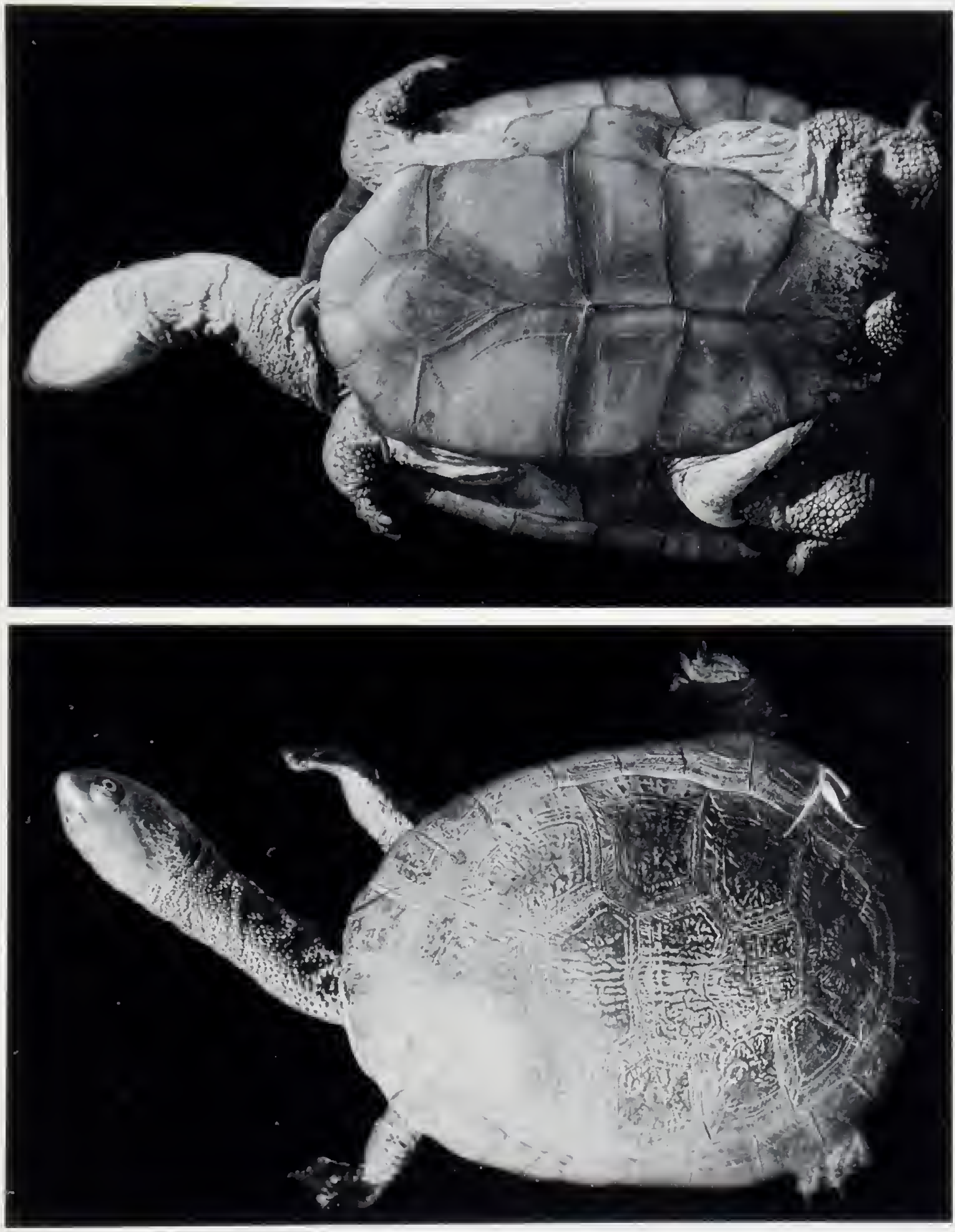

Figure 1. Dorsal and ventral views of Holotype of *Chelodina pritchardi* (MCZ 173543, sub-adult male measuring 129.5 mm carapace length) from Bore, Kemp Welch River, Central Province, Papua New Guinea, photographed while still alive.

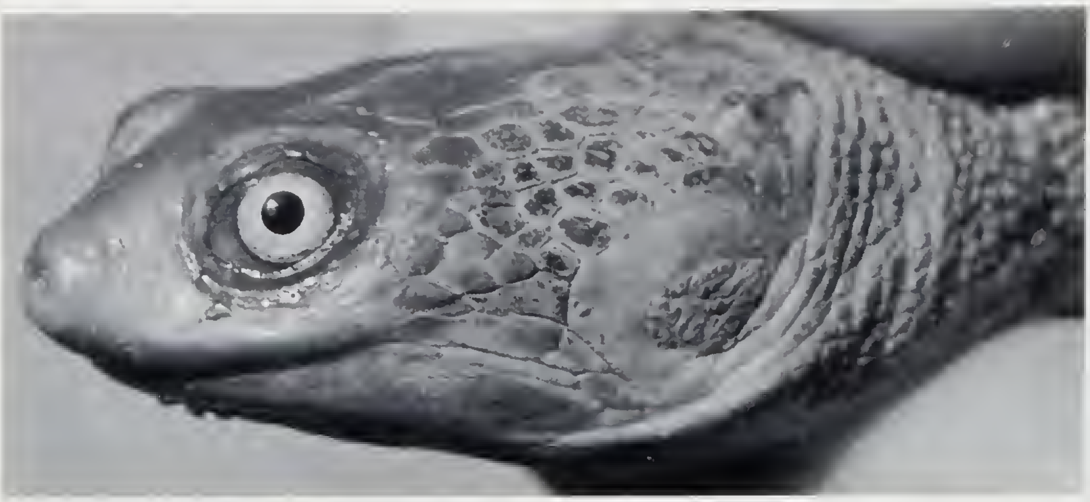

Figure 2. Lateral head view of Holotype of *Chelodina pritchardi* (MCZ 173543). Note the striking light-colored iris.

Distribution. The species is known definitively only from the Kemp Welch River drainage basin southeast of Port Moresby, Central Province, Papua New Guinea, an area of relatively high rainfall and mesic lowland alluvial forests (Fig. 4). It appears to be absent from the Port Moresby region itself, an area of low rainfall and xeric savannah vegetation. It is not yet known whether the range also extends further southeast along the coast toward Cape Rodney and Abau, where appropriate wetland habitat also occurs. The species may additionally occur in the mesic lowland coastal plain northwest of Port Moresby in the Laloki River area, where reports tentatively suggest its presence.

Diagnosis. A medium-sized New Guinean snake-necked chelid turtle of *Chelodina* subgeneric group "A" (Burbidge *et al.,* 1974) with relatively narrow head and wide plastron (Fig. 5), superficially resembling *C. novaeguineae* but more closely related to Australian *C. longicollis.* Plastral and head widths intermediate between *C. novaeguineae* and *C. longicollis* (Fig. 6). Skull osteology distinctive: narrow maxillary and mandibular triturating surfaces with decreased anterior skull robusticity; decreased temporal fossa muscular volume with increased parietal roof width. Skull most similar to *C. longicollis,* markedly divergent from *C. novaeguineae* and *C. reimanni,* both of which have significantly more robust skulls. Eye unicolor light tan, pale plastron often with

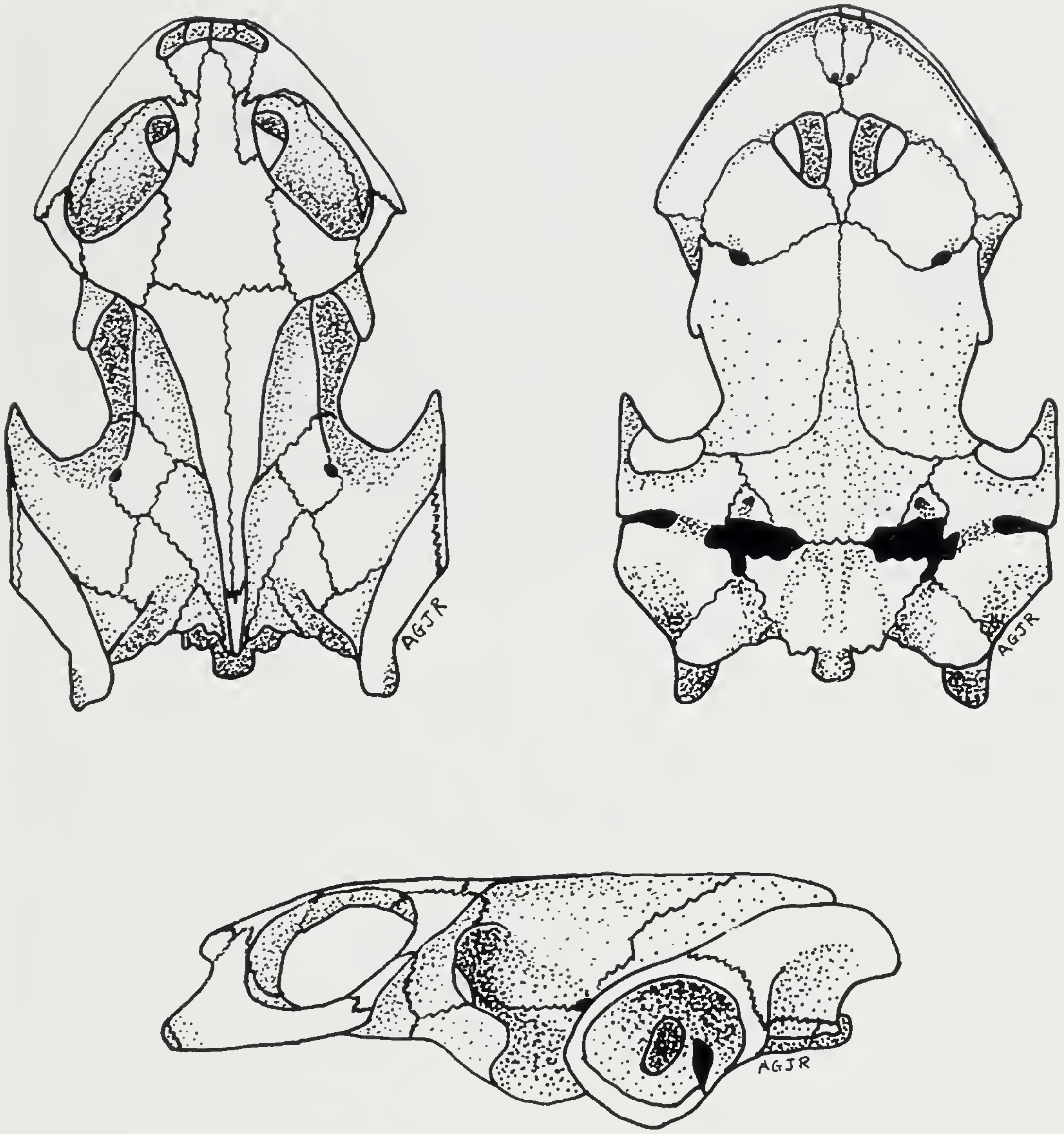

Figure 3. Dorsal, ventral, and lateral views of skull of *Chelodina pritchardi* (Paratype AMNH 139735, adult female measuring 193 mm carapace length) from nr. Hula, Kemp Welch River, Central Province, Papua New Guinea.

darker color pattern following midline sutures broadly. Eggs relatively smaller than any other *Chelodina.*

Etymology. The specific epithet is a patronym honoring Dr. Peter C. H. Pritchard, well-known turtle authority, close professional colleague, and personal friend, who serendipitously obtained the first two specimens while on a marine turtle consultancy in Papua New Guinea.

TABLE 1. BASIC EXTERNAL DIMENSIONS OF *CHELODINA PRITCHARDI*. ALL MEASUREMENTS IN MM. CL = CARAPACE LENGTH (STRAIGHT-LINE IN MIDLINE); CW = CARAPACE WIDTH (GREATEST); CD = CARAPACE DEPTH (GREATEST IN MIDLINE); PL-M = PLASTRON LENGTH (ALONG MIDLINE, NOT INCLUDING ANAL SPURS); PL-T = PLASTRON LENGTH (MAXIMUM, INCLUDING ANAL SPURS); PW = PLASTRON WIDTH (AT AXILLARY NOTCH); HW = HEAD WIDTH (TYMPANIC).

Specimen Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW
AGJR-T 1643	f	125.0	96.5	40.0	98.0	104.5	59.5	20.2
MCZ 173543	m	129.5	100.0	41.0	103.5	109.5	60.5	20.5
AGJR-T 1583	j	134.7	106.5	44.4	106.0	112.4	63.3	21.0
AGJR-T 1601	m	136.0	106.0	44.5	108.0	114.5	64.5	21.2
AGJR-T 1608	m	139.0	112.5	45.5	112.0	117.5	67.0	21.8
AGJR-T 1589	m	140.0	111.0	45.0	111.5	118.4	66.5	21.5
AGJR-T 1593	m	140.5	112.0	47.0	111.5	118.0	68.0	22.0
AGJR-T 1592	m	141.0	108.0	44.5	112.0	118.0	65.0	21.6
AGJR-T 1600	m	142.5	107.5	45.5				21.8
AGJR-T 1602	m	143.5	111.0	47.5	111.0	119.0	68.0	22.0
AGJR-T 1588	m	145.0	113.5	46.3	115.0	122.0	68.2	22.4
AGJR-T 1590	m	145.5	113.7	48.2	115.5	122.0	70.0	22.5
AGJR-T 1599	m	146.5	115.0	46.5				22.5
AGJR-T 1585	m	150.0	117.0	49.0	115.0	124.0	70.5	22.3
AGJR-T 1607	m	150.0	115.0	48.0	115.0	123.0	72.0	22.6
AGJR-T 1577	m	150.7	117.0	47.0	116.0	125.0	71.0	22.4
AGJR-T 1591	m	152.0	121.0	50.5	119.0	127.5	72.0	22.5
AGJR-T 1644	m	153.5	125.0	50.0	121.0	129.0	73.5	22.9
AGJR-T 1580	m	156.0	125.0	51.4	122.0	131.0	74.5	23.0
AGJR-T 1609	m	156.5	124.5	48.0	122.0	131.0	74.0	23.5
AGJR-T 1575	m	156.8	123.3	52.8	121.0	129.8	75.4	23.9
AGJR-T 1594	m	157.0	125.0	53.0	121.5	129.0	75.0	24.3
AGJR-T 1595	f	157.0	121.5	52.5	123.0	131.0	74.5	23.8
AGJR-T 1646	f	157.0	128.5	55.0	125.5	132.5	76.5	23.0
AGJR-T 1587	f	157.5	121.0	49.0	119.5	128.0	74.0	23.4
AGJR-T 1645	m	160.0	126.5	52.0	124.5	133.0	79.0	23.8
AGJR-T 1582	m	160.2	122.5	51.2	121.7	131.2	75.5	24.3
AGJR-T 1586	m	160.5	123.5	51.5	122.5	133.0	75.5	24.2
AGJR-T 1598	m	161.0	131.0	52.5				23.8
AGJR-T 1606	m	161.0	125.5	53.0	123.0	133.0	77.5	23.8
PNGM 23373	f	162.0	118.0	52.0	126.0		76.0	25.0
AGJR-T 1605	m	163.5	131.5	54.5	128.5	139.0	79.0	24.8
AGJR-T 1581	m	163.8	127.8	54.2	127.0	137.7	78.0	24.6
AGJR-T 1603	m	165.0	128.0	53.5	126.5	136.5	77.0	24.7
AGJR-T 1576	m	165.4	131.5	51.8	126.3	137.3	78.0	24.5
AGJR-T 1604	m	168.0	128.5	56.0	127.0	136.5	78.0	25.3
AGJR-T 1596	f	171.0	133.0	57.5				25.0

TABLE 1. Continued.

Specimen Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW
AGJR-T 1597	f	175.5	138.0	59.0				25.5
AGJR-T 1584	m	186.4	143.8	63.7	140.0	151.5	87.8	27.5
AMNH 139735	f	193.0	156.0	62.0	154.0		93.5	27.0
AGJR-T 1578	f	199.3	161.4	65.5	157.5	166.0	97.4	28.4
AGJR-T 1579	f	206.0	167.0	69.5	158.0	169.0	99.0	29.0
MCZ 175813	f	228.0	180.0	90.0	183.0		107.0	31.0

Related Taxa. Chelodina pritchardi is most similar to the following four chelid taxa from New Guinea and Australia (all members of *Chelodina* subgeneric group "A").

Chelodina longicollis (Shaw, 1794). Original designation *Testudo longicollis.* Type locality "New Holland" [=Australia]. Holotype BMNH 1947.3.5.86, a dry specimen of 134 mm carapace length.

Chelodina novaeguineae Boulenger, 1888. Original designation *Chelodina novaeguineae.* Type locality "Katow, S.E. New Guinea" [= Mawatta, Binaturi River, Western Province, Papua New Guinea]. Original syntypes BMNH 1946.1.22.36 and MCG CE 8407, collected by L. M. d'Albertis. BMNH 1946.1.22.36, a subadult female of 137 mm carapace length figured by Boulenger, 1889 (plates 5, 6) and photographed in this paper (Fig. 7) is hereby confirmed as lectotype (previously designated by Wells and Wellington, 1985, p. 8).

Chelodina reimanni Philippen and Grossman, 1990. Type locality "Merauke-River, West-Irian, Neuguinea" [= Merauke River, Irian Jaya, Indonesia]. Holotype MTKD 29178, adult female of 180 mm carapace length, collected by Frank Yowono, 1988.

Chelodina steindachneri Siebenrock, 1914. Type locality "Marloo Station am Grey River in Westaustralien" [Western Australia, Australia]. Holotype NMW 19798 (Naturhistorisches Museum Wien).

DESCRIPTION

External Morphology

Carapace. Carapace of *C. pritchardi* smooth and broadly oval, width averaging 78.5% of length, moderately flared posteriorly with marginals 6–9 somewhat expanded. No lateral marginal recurving. No vertebral knobs or keel. Slight vertebral flattening or shallow furrow in some specimens. No supracaudal notch or marginal serrations. Dorsal nuchal long and broad, slightly protruding beyond anterior carapace edge in smaller specimens. Ventral un-

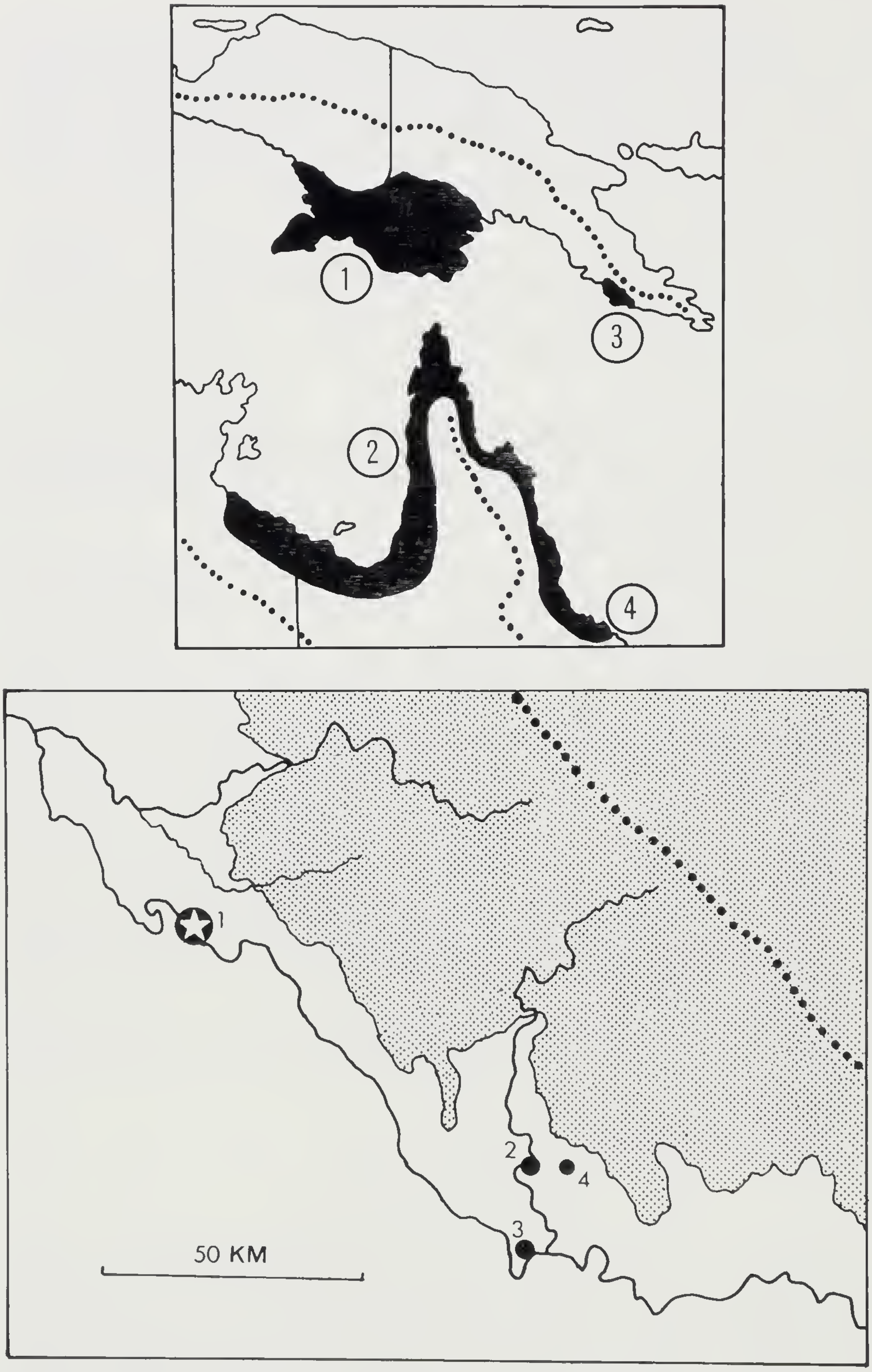

Figure 4. Top: Distribution of *Chelodina pritchardi, C. novaeguineae,* and *C. longicollis.* 1. New Guinean distribution of *C. novaeguineae* in Irian Jaya and Papua New Guinea. 2. Australian distribution of *C. novaeguineae* in Northern

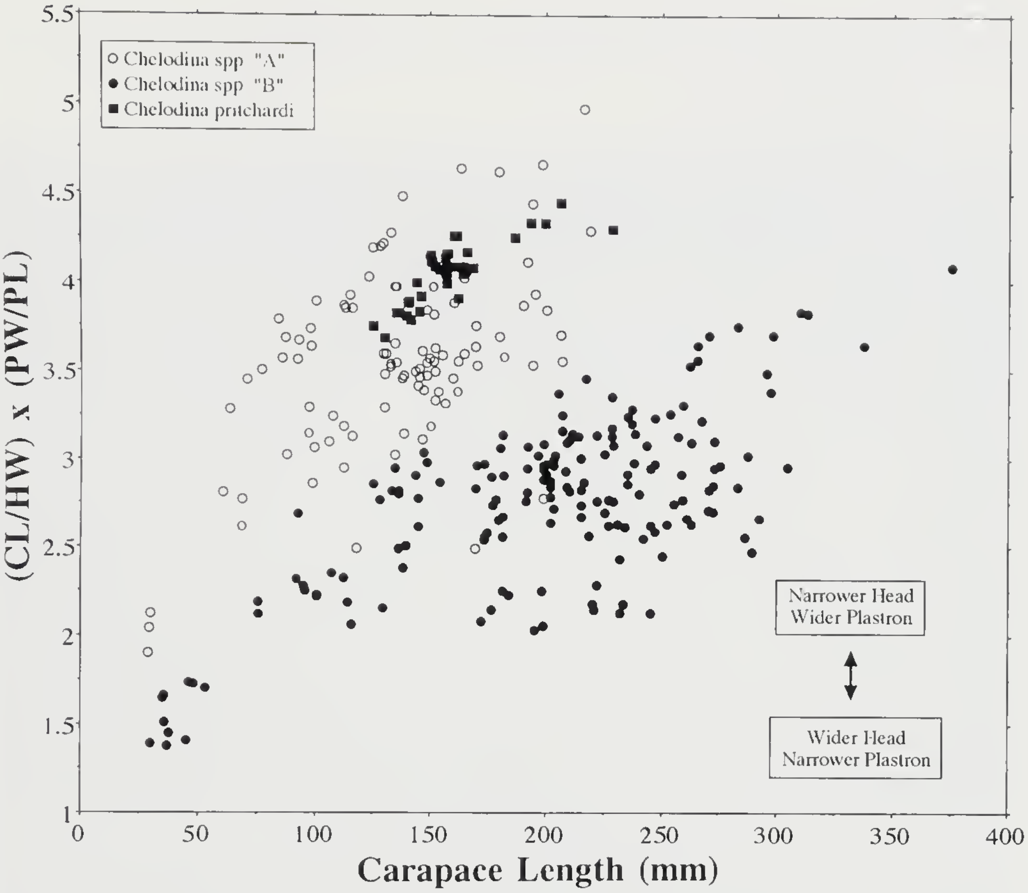

Figure 5. Scattergram plotting the relationships of head width ratio (Carapace Length/Head Width) and plastron width ratio (Plastron Width/Plastron Length), expressed as a bivariate product, versus carapace length for the subgeneric groups of *Chelodina* (*Chelodina* "A" = *C. longicollis, C. novaeguineae, C. pritchardi, C. steindachneri,* and *C. reimanni, Chelodina* "B" = *C. expansa, C. oblonga, C. parkeri, C. rugosa,* and *C. siebenrocki*). Note the position of *C. pritchardi* within the *Chelodina* "A" generic grouping. Note also the three specimens of subgeneric group "A" within the group "B" area; these represent extremely broad-headed *C. reimanni.*

⟵

Territory and Queensland. 3. Distribution of *C. pritchardi* in Papua New Guinea. 4. Approximate northern limit of the distribution of *C. longicollis* in eastern Australia. Major watershed limits indicated as heavy dotted lines. Bottom: Area 3 of top map enlarged here and showing distribution of *Chelodina pritchardi* in the Port Moresby region, Central Province, Papua New Guinea. The shaded area represents elevation above 200 m, the heavy dotted line shows the watershed limit of the Owen Stanley Ranges. Starred locality (1) is Port Moresby. Black dots represent localities for *C. pritchardi* in the Kemp Welch River basin, as follows: (2) Bore, Kemp Welch River; (3) Hula; (4) ca. 10 km east of Bore.

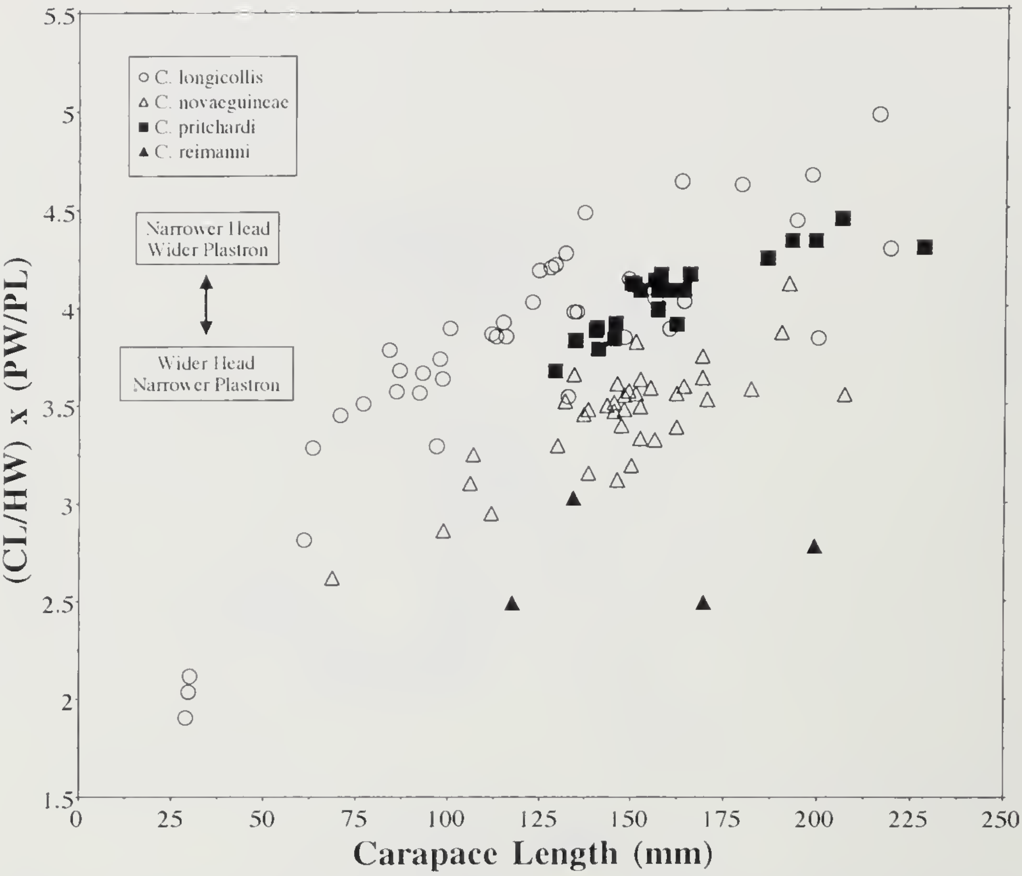

Figure 6. Scattergram plotting the relationships of head width ratio (Carapace Length/Head Width) and plastron width ratio (Plastron Width/Plastron Length), expressed as a bivariate product, versus carapace length in four species of *Chelodina*. Note that *C. pritchardi* is essentially intermediate between *C. longicollis* and *C. novaeguineae*, but more similar to *C. longicollis*.

derlap of nuchal also relatively long and broad. Vertebral 1 widest, then 2, 3, 5, and 4 in descending order of width. Carapace somewhat broader in *C. pritchardi* than in New Guinean *C. novaeguineae,* intermediate in *C. longicollis,* significantly narrower in *C. reimanni* (see Fig. 8 and Table 2).

Carapace moderately deep in older specimens, relatively flatter in younger ones. No sexual dimorphism in carapace depth in specimens examined. Carapacial scutes lightly rugose with partially retained growth lines until mid-adult size.

Color dark chestnut brown. Carapace very similar to both *C. novaeguineae* and *C. longicollis,* but generally more broad than *C. novaeguineae* and slightly less broad than *C. longicollis.* Carapace superficially more similar to *C. novaeguineae* than to *C. longicollis* (Figs. 1 and 7).

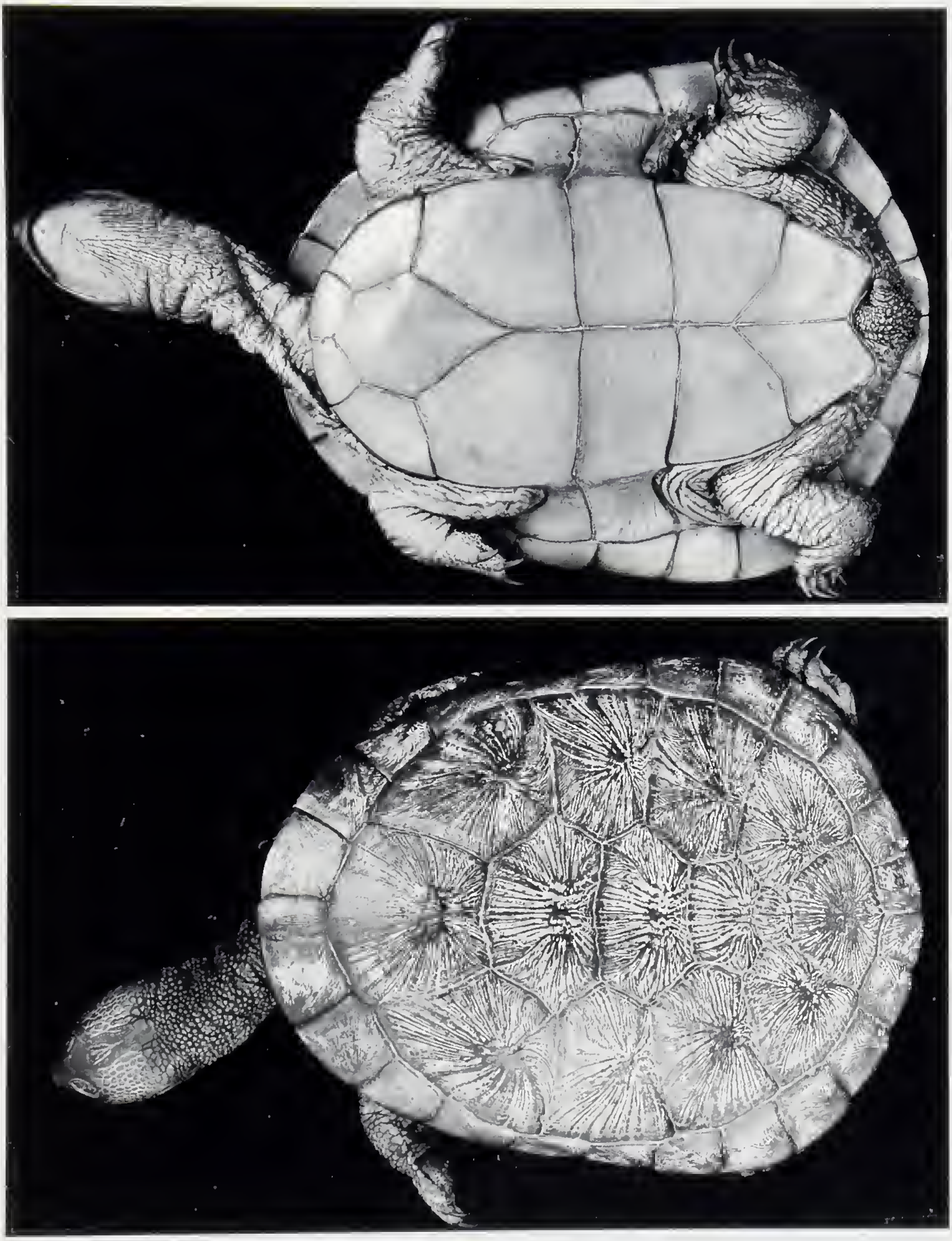

Figure 7. Lectotype of *Chelodina novaeguineae* (BMNH 1946.1.22.36, sub-adult female measuring 137 mm carapace length), from Katow, S.E. New Guinea [= Mawatta, Binaturi River, Western Province, Papua New Guinea].

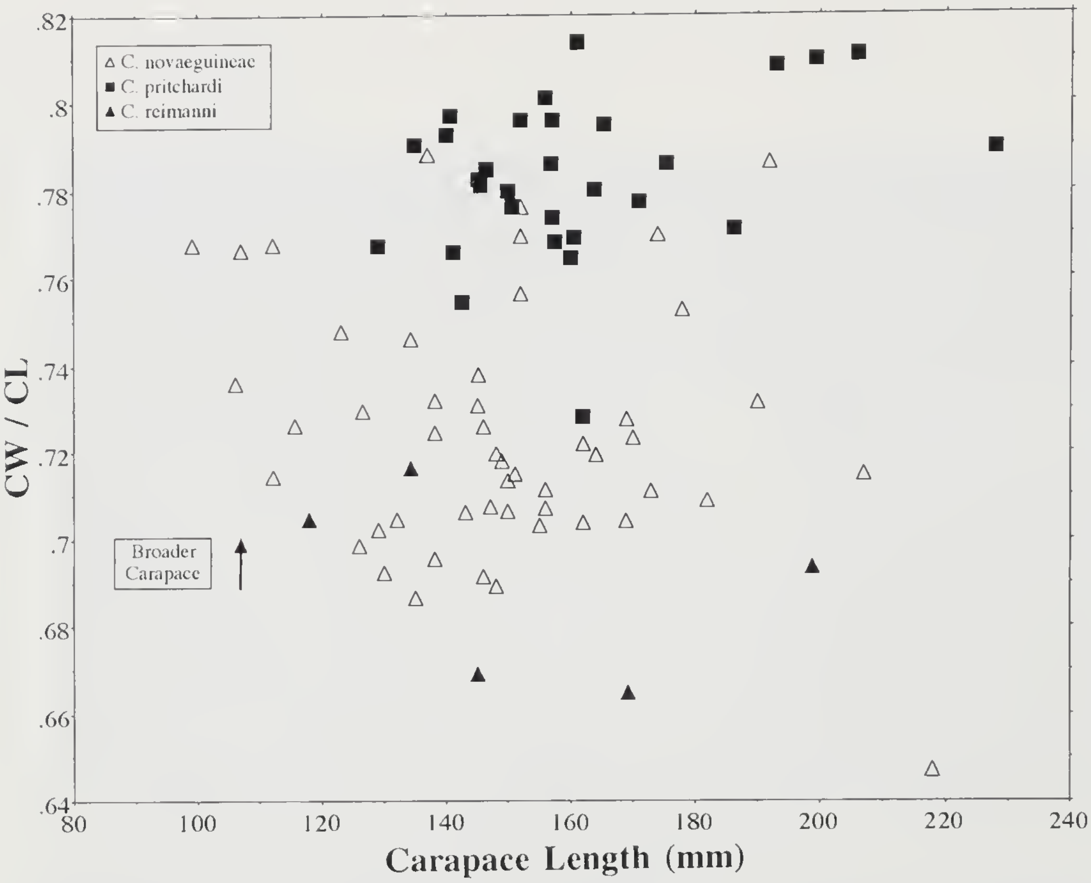

Figure 8. Scattergram plotting carapace width ratio (CW/CL) versus carapace length in three species of *Chelodina,* utilizing data only from New Guinean specimens of greater than 100 mm carapace length. Note the broader carapace in *C. pritchardi.*

Plastron. Plastron broad, axillary width averaging 61% of midline length, anterior lobe moderately broad, intermediate between the relatively narrow tapered lobe of *C. novaeguineae* and *C. reimanni,* and the broadly expanded anterior lobe of *C. longicollis* (Fig. 6 and Table 2). Slight secondary expansion of anterior plastral lobe at posterior border of humeral scutes, not present in *C. novaeguineae.* Anal notch moderately deep, no sexual dimorphism noted. Intergular broad, long, and recessed without marginal contact. Plastral scute suture length formula: Ig > An > Abd > Pec > Fem > Gul. No axillary or inguinal scutes.

Plastral color yellow with variable amount of light to moderate brown pigment following central portions of sutures broadly, often expanding to cover much of central plastron. Holotype plastron oxidized to darker brown. Plastral color different from *C.*

TABLE 2. MEANS AND STANDARD DEVIATIONS FOR SHELL MEASUREMENT RATIOS OF FOUR *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 1. DATA BASED ONLY ON SPECIMENS OF CARAPACE LENGTH GREATER THAN 100 MM. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NO AUSTRALIAN ONES.

Feature	*C. longicollis* (n = 37)	*C. pritchardi* (n = 43)	*C. novaeguineae* (n = 51)	*C. reimanni* (n = 5)
CW/CL	.775 ± .042	.785 ± .018	.723 ± .028	.690 ± .022
PW/PL-M	.618 ± .026	.610 ± .012	.576 ± .018	.543 ± .028
HW/CL	.151 ± .012	.150 ± .005	.167 ± .010	.202 ± .012
CD/CL	.310 ± .026	.328 ± .014	.327 ± .021	.315 ± .007

novaeguineae, which usually has an immaculate yellow plastron with occasional very thin pigment lines following the sutures, and from *C. longicollis,* which usually has broad black color zones along the sutures and sometimes over most of the plastron. Plastron superficially more similar to *C. novaeguineae* than to *C. longicollis* (Figs. 1 and 7).

Head and Soft Parts. Head with small irregular scales covering temporal skin, smooth over parietal and interorbital roof. Neck with low soft tubercles, less pronounced than the larger raised firmer tubercles of *C. novaeguineae.* Soft parts grayish-brown dorsally, yellowish-white ventrally. Hands and feet with 4 claws each.

Head width narrow, typical of *Chelodina* subgeneric group "A" species (Fig. 5), intermediate between the wider heads of *C. novaeguineae* and *C. reimanni* and the narrower head of *C. longicollis* (Fig. 6). Relative width of head narrows ontogenetically.

Eye color of *C. pritchardi* primarily light tan with medium dark tan thin area at outer periphery of iris and very light tan thin inner rim, becoming nearly white along the pupillary edge of the iris. No color flecks or cross-bar. Eye color of *C. novaeguineae* from Papua New Guinea (personal observation) and Australia (Cann, 1978: plate 19) dark brown with more sharply distinct yellowish-white pupillary rim around inner iris, and dark area of iris with multiple small irregular flecks of darker and lighter pigment. Overall impression of eye color of *C. pritchardi* unicolor whitish-tan, of *C. novaeguineae* bicolor dark brown with inner yellow circle.

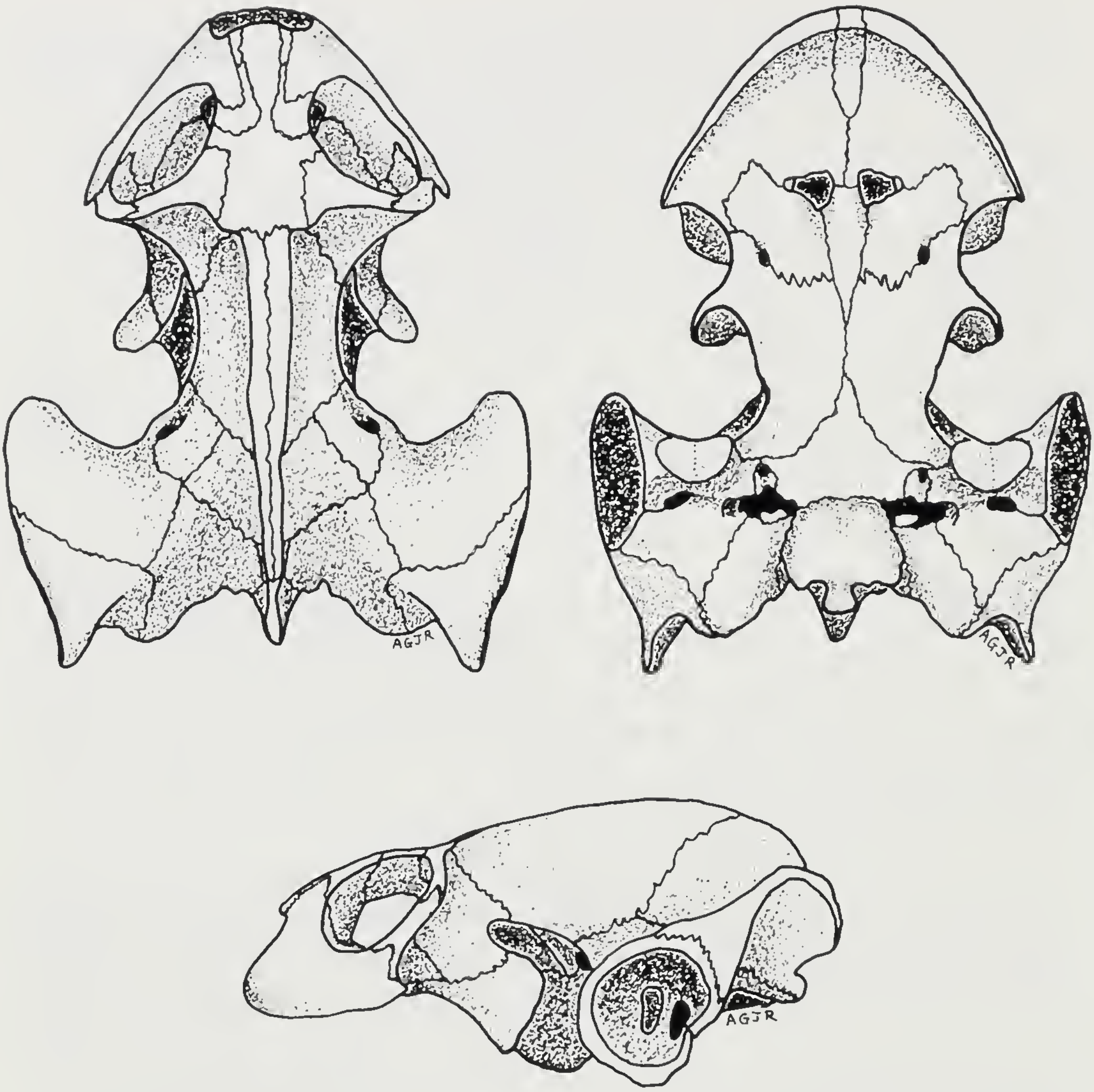

Figure 9. Dorsal, ventral, and lateral views of skull of *Chelodina reimanni* (AGJR-T 746, 199 mm carapace length female from Merauke, Irian Jaya, Indonesia).

Size and Sexual Dimorphism. The largest specimen of *C. pritchardi* recorded is a female of 228 mm carapace length. The largest male examined has a carapace length of 186 mm, indicating probable sexual dimorphism, with females larger than males. Calculating the sexual dimorphism index according to the method of Gibbons and Lovich (1990) yields an SDI value of approximately 1.22 for *C. pritchardi.* The SDI value for New Guinean *C. novaeguineae* is approximately 1.37, with the largest confirmed female measuring 207 mm and the largest male 151 mm.

The largest specimen of New Guinean *C. novaeguineae* I ex-

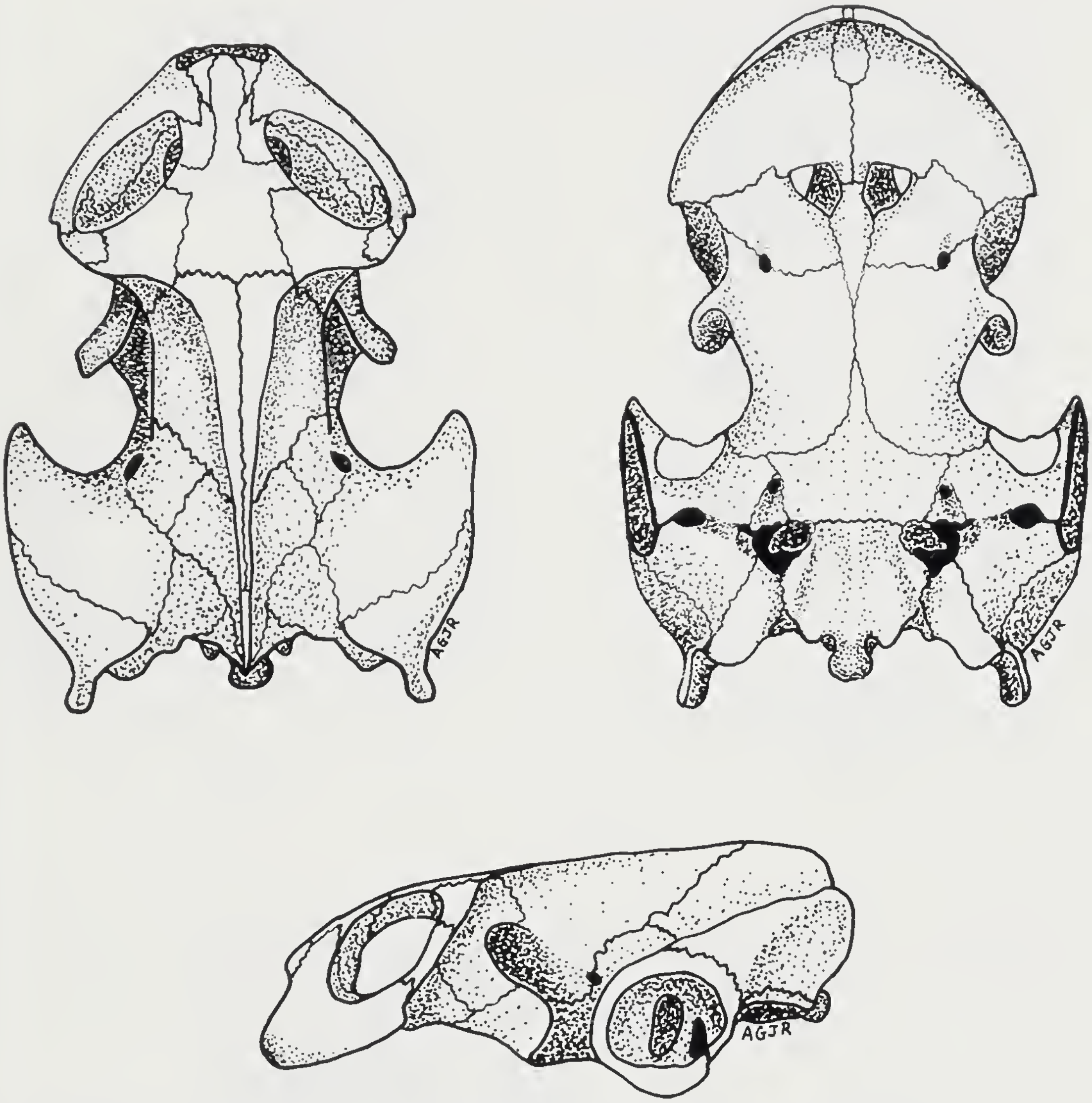

Figure 10. Dorsal, ventral, and lateral views of skull of *Chelodina novaeguineae* (AGJR-T 504, 178 mm carapace length female from Boze, Binaturi River, Western Province, Papua New Guinea).

amined was a female measuring 207 mm, but Philip Hall (personal communication) has photographed and measured a 218 mm specimen from the Irian Jaya-Papua New Guinea border. The largest specimen of Australian *C. novaeguineae* I examined measured 279 mm, but Cann (1978) records 300 mm as the maximum size. The largest specimen of *C. reimanni* I examined measured 199 mm, but Philippen and Grossman (1990) records 206 mm as the maximum size. In general, *C. pritchardi* is larger than New Guinean *C. novaeguineae* or *C. reimanni,* and smaller than Australian *C. novaeguineae.*

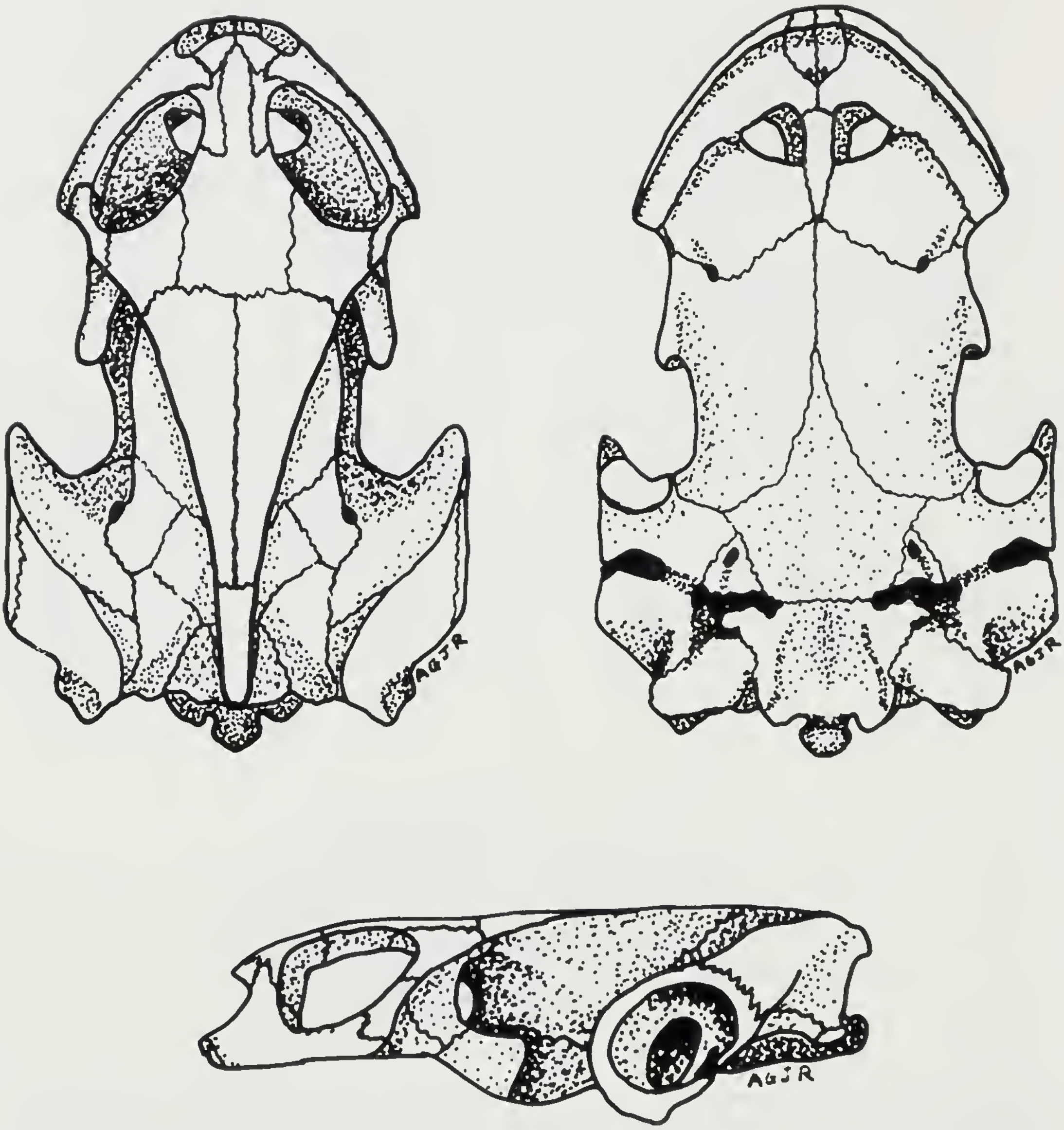

Figure 11. Dorsal, ventral, and lateral views of skull of *Chelodina longicollis* (AMNH 108952, from Patho, Victoria, Australia).

Osteology

Skull. The description of skull osteology is based on the examination of 6 skulls of *C. pritchardi.* Comparison is performed with skulls of 7 *C. longicollis,* 15 *C. novaeguineae* (12 from New Guinea, 3 from Australia), and 2 *C. reimanni.* Refer to Figures 3 and 9–11 for skull illustrations of the four species and Tables 3 and 4 and Figures 12–14 for additional skull measurements and ratios.

The skull of *C. pritchardi* is a typical *Chelodina* subgeneric group "A" type skull, not overly elongate, flattened, or wide as

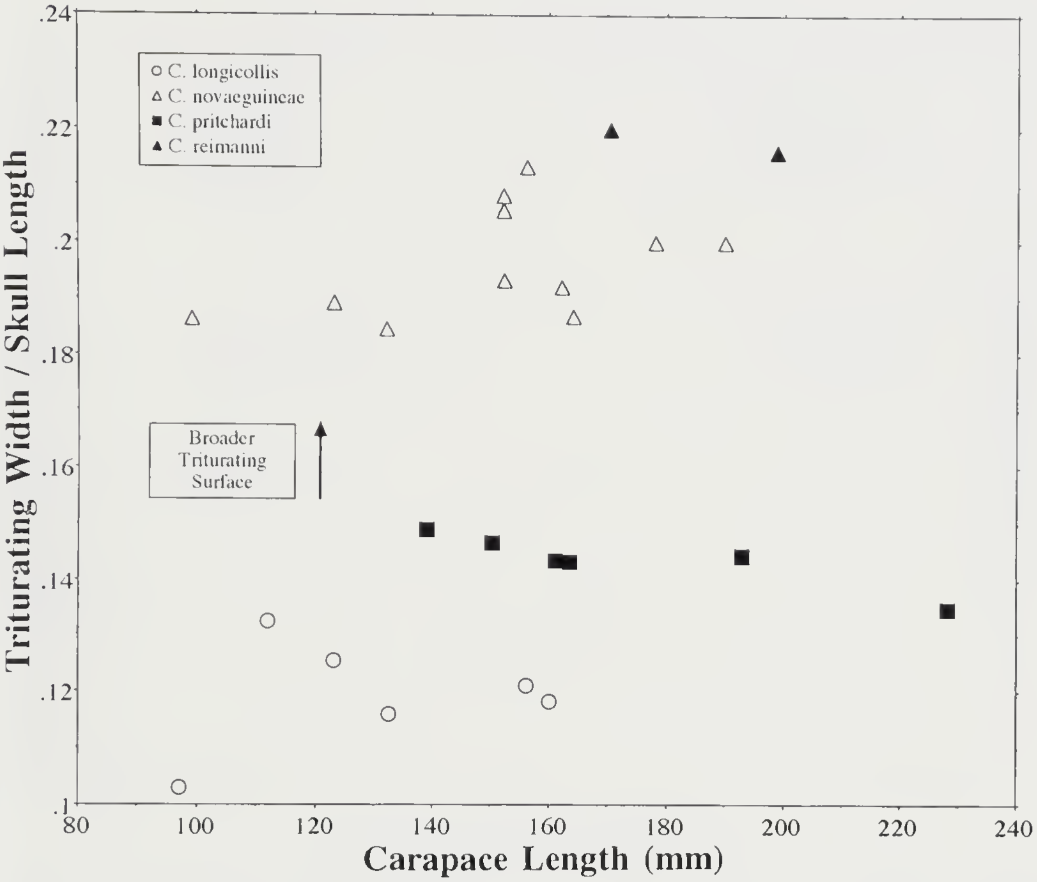

Figure 12. Scattergram plotting maxillary triturating surface width ratio (TW/SL) versus carapace length in four species of *Chelodina.* Note the much broader triturating surface in *C. novaeguineae* and *C. reimanni* with *C. pritchardi* being somewhat intermediate and *C. longicollis* much narrower.

in subgeneric group “B”. It is strikingly similar to the skull of *C. longicollis,* from which it is differentiated by only a few features. It differs markedly from its more geographically proximate congeners *C. novaeguineae* and *C. reimanni.*

The major differentiating features involve the width and robusticity of the triturating surfaces and the relative volume of the muscular temporal fossa. *C. novaeguineae* and *C. reimanni* have wide and robust maxillary and mandibular triturating surfaces, with correspondingly wide and robust horny rhamphothecae. *C. longicollis* has very narrow and weak surfaces and *C. pritchardi* is intermediate (Fig. 12), but more similar to *C. longicollis.* The mandibular coronoid process is high and prominent in *C. novaeguineae* and *C. reimanni,* low and less prominent in *C. longicollis,* and intermediate in *C. pritchardi. C. novaeguineae* and

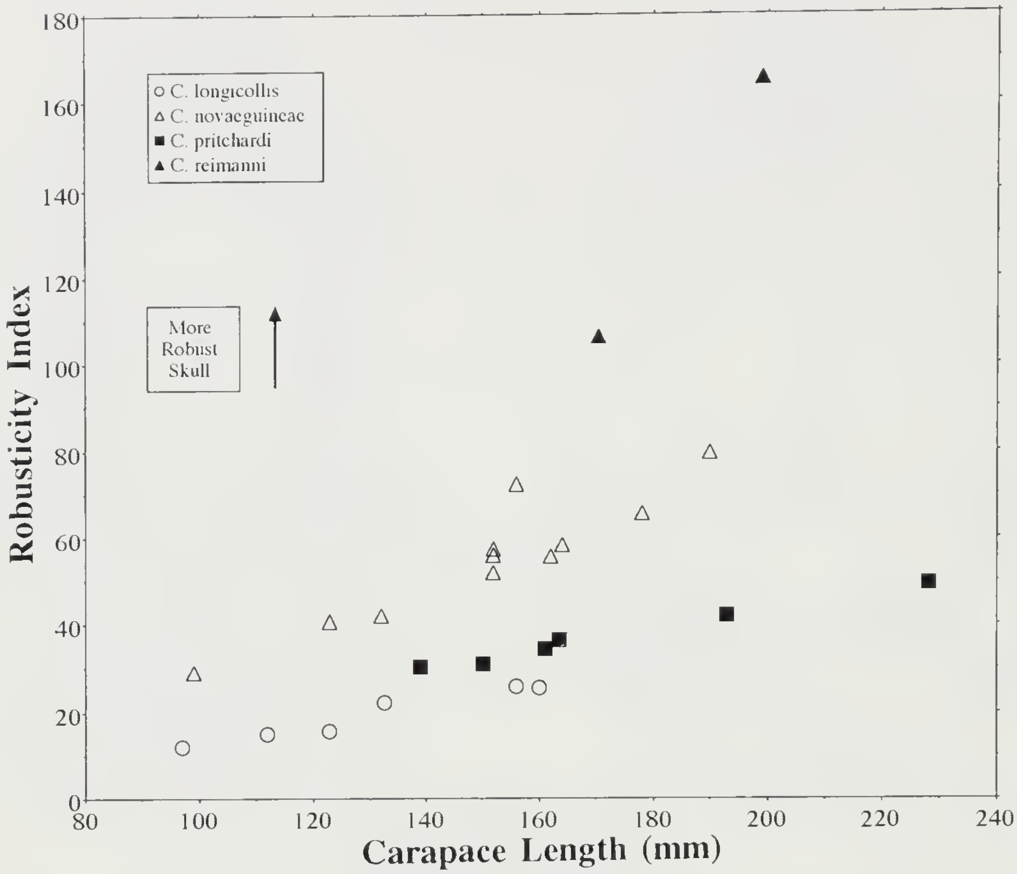

Figure 13. Scattergram plotting skull Robusticity Index [RI = (TW × SWT × SD)/SL] versus carapace length in four species of *Chelodina.* Note the intermediate position of *C. pritchardi* with reference to the other species.

C. reimanni have a long midline maxillary suture, reflecting the increased width of the maxillary triturating surface; both *C. longicollis* and *C. pritchardi* have short sutures.

The relative position of the choanae is posterior in *C. novaeguineae* and *C. reimanni,* anterior in *C. longicollis* and *C. pritchardi,* once again as a result of the widened triturating surface. The vomer is more robust, wider, and reaches further posterior in *C. novaeguineae* and *C. reimanni* than in *C. longicollis* or *C. pritchardi.* It reaches the level of the palatine foramen and separates the palatines widely in *C. novaeguineae* and *C. reimanni,* does not reach the level of the palatine foramen and only barely separates the palatines in *C. longicollis* and *C. pritchardi.* In *C. novaeguineae* and *C. reimanni* the pterygoids do not extend anteriorly along the midline to meet the vomer anterior to the palatine foramen, in *C. longicollis* and *C. pritchardi* the pterygoids do extend anteriorly.

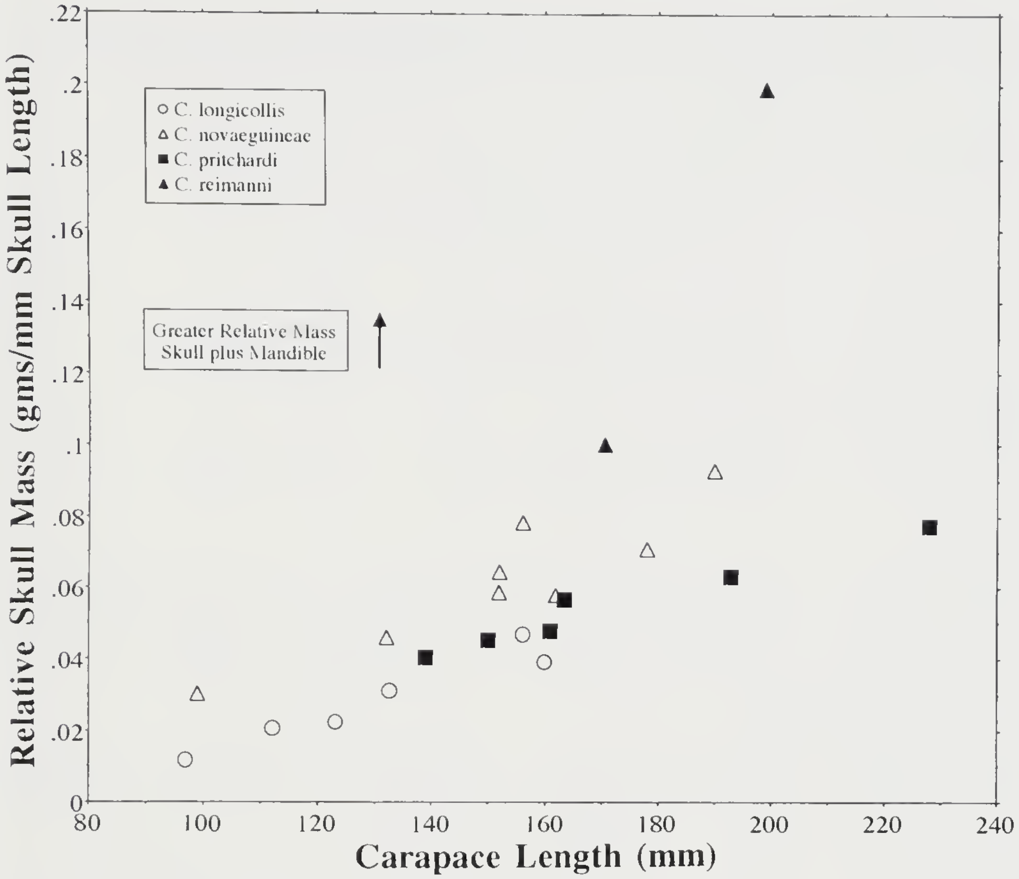

Figure 14. Scattergram plotting relative skull mass (skull and mandible weight in gms/skull length in mm) versus carapace length in four species of *Chelodina*. Note the intermediate position of *C. pritchardi* with reference to the other species, with *C. reimanni* and *C. novaeguineae* having heavier, more robust skulls.

The shape of the anterior skull tomial edge also differs, with *C. novaeguineae* and *C. reimanni* having a somewhat rounded, blunted shape, and *C. longicollis* and *C. pritchardi* slightly more angular. The premaxillae are usually fused into a single small premaxilla in New Guinean *C. novaeguineae* (11 of 12 skulls) and *C. reimanni* (2 of 2); unfused but very small in Australian *C. novaeguineae* (3 of 3), and unfused and large in *C. longicollis* and *C. pritchardi*. Premaxillary foramina are absent in New Guinean *C. novaeguineae* and *C. reimanni*, reduced but present in Australian *C. novaeguineae*, and well-developed in *C. longicollis* and *C. pritchardi*.

The ventral view of the skull reveals that the posterior extension of the quadrate beyond the posterior extension of the opisthotic differs between the species. *C. novaeguineae, C. reimanni,* and *C. pritchardi* have prominent quadrate extensions, *C. longicollis* does

Table 3. Basic skull measurements for four species of Chelodina. SL = skull length (snout–occipital condyle); SWT = skull width, tympanic maximum; SWM = skull width, maxillary maximum; SDM = skull depth at posterior edge of maxillae; SD = skull depth in midline between supraoccipital spine and basisphenoid; IOW = inter-orbital width, minimal; OW = orbital width, short axis; PtW = pterygoid width, minimal; TW = triturating width, maxillary (measured in midline from tomial edge to anterior choanal border). Refer to Table 4 and Figures 12 and 13 for analysis of skull measurement ratios.

Species Mus. Sp. No.	SL	SWT	SWM	SDM	SD	IOW	OW	PtW	TW
Chelodina longicollis									
AGJR-T 159	25.2	16.1	12.8	5.9	7.1	2.4	6.0	8.8	2.6
MCZ 8369	26.4	16.8	12.4	5.0	6.7	2.5	5.5	8.7	3.5
MCZ 8377	27.1	17.9	13.0	6.0	7.0	2.4	5.8	9.4	3.4
AGJR-T 158	33.6	21.6	17.0	7.3	8.9	3.4	7.0	11.1	3.9
MCZ 86783	35.5	23.4	18.6	7.6	9.2	3.5	7.5	11.0	4.2
AGJR-T 179	36.3	23.2	18.9	8.2	9.2	4.3	7.8	12.0	4.4
AMNH 108952	40.5	25.1	20.2	8.2	10.1	3.5	8.3	13.9	4.6
Chelodina novaeguineae									
MCZ 134394	26.3	17.8	13.3	6.6	8.8	3.0	6.3	8.4	4.9
AMNH 57589	31.2	21.0	16.3	8.0	10.3	3.6	7.5	9.7	5.9
MCZ 134712	32.5	22.4	16.5	7.7	10.2	3.8	7.3	10.5	6.0
UU 14716	33.7	23.0	18.2	7.2	9.5			11.2	6.3
MCZ 134391	35.0	23.3	17.7	8.2	11.7	4.6	7.0	10.5	7.2
AMNH 117939	35.7		18.5		11.5	4.3	7.5	11.2	6.9
MCZ 134395	35.7	24.0	18.0	9.0	11.2	4.7	7.8	11.8	6.9
MCZ 134390	36.5	24.4	18.9	8.5	11.3	4.6	7.6	11.5	7.6
MCZ 134392	37.0	26.0	20.0	9.5	13.0	4.8	8.6	12.2	7.9
AGJR-T 504	38.0	26.4	20.7	9.0	12.4	4.8	8.0	11.4	7.6
MCZ 134393	38.0	26.0	20.0		12.0	5.0	8.0	12.0	7.1
MCZ 134396	38.0	25.0	19.0		11.6	4.4	8.0	11.0	7.3
MCZ 142495	41.0	27.6	22.2	9.6	14.4	5.6	8.9	12.5	8.2
AMNH 86547	46.0	34.0	27.8	10.6	14.2	5.6	9.8	15.5	8.4
AMNH 86544	50.7	37.3	30.3	12.2	15.4	5.4	10.3	16.2	9.5
Chelodina pritchardi									
AGJR-T 1608	32.2	20.8	18.0	7.6	9.8	3.3	7.5	10.6	4.8
AGJR-T 1607	34.1	21.6	18.7	7.7	9.8	3.6	7.9	11.3	5.0
AGJR-T 1606	35.5	22.8	19.8	8.3	10.5	4.1	8.4	12.1	5.1
AGJR-T 1605	37.0	23.8	20.5	8.8	10.7	4.0	8.4	12.1	5.3
AMNH 139735	39.5	26.5	21.5	8.8	11.0	4.5	8.5	13.6	5.7
MCZ 175813	44.5	29.0	24.8	10.0	12.6	4.5	10.5	15.8	6.0
Chelodina reimanni									
AGJR-T 1614	42.9	30.7	23.1	10.6	16.0	6.5	9.0	13.4	9.3
AGJR-T 746	47.7	39.5	28.4	13.5	19.4	7.3	10.6	12.2	10.3

TABLE 4. MEANS AND STANDARD DEVIATIONS FOR SKULL MEASUREMENT RATIOS OF FOUR *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 3.

Feature	*C. longicollis* (n = 7)	*C. pritchardi* (n = 6)	*C. novaeguineae* (n = 15)	*C. reimanni* (n = 2)
SWT/SL	.642 ± .014	.648 ± .013	.687 ± .024	.774 ± .076
SWM/SL	.501 ± .020	.553 ± .006	.532 ± .032	.568 ± .039
SD/SL	.260 ± .011	.290 ± .009	.320 ± .018	.388 ± .026
TW/SL	.119 ± .009	.144 ± .005	.194 ± .009	.218 ± .003
PtW/SWT	.521 ± .027	.522 ± .014	.461 ± .018	.372 ± .090
IOW/OW	.456 ± .052	.470 ± .037	.570 ± .055	.705 ± .024

not. This represents a major difference between the otherwise somewhat similar skulls of *C. pritchardi* and *C. longicollis.* The pterygoid trochlear processes are prominent and markedly divergent in *C. novaeguineae* and *C. reimanni,* with New Guinean specimens exhibiting prominent flaring, while Australian ones exhibit none; the processes are minimally divergent and much less prominent in *C. longicollis* and *C. pritchardi.* The ventral view of the skull shows the flared pterygoid processes are very prominent in New Guinean *C. novaeguineae* and *C. reimanni,* less prominent in the other species. Also, on the ventral view of the skull, the postorbital portions of the jugal and postorbital are well seen in *C. novaeguineae* and *C. reimanni,* but not in *C. longicollis* or *C. pritchardi.*

The parietal roof extent and shape differ markedly between the four species. *Chelodina reimanni* has an extremely narrow parietal crest, with nearly complete temporal emargination, *C. novaeguineae* also has an extremely narrow parietal crest, but with very slightly less emargination, *C. longicollis* has a fairly wide triangular parietal roof, with much less temporal emargination, and *C. pritchardi* is intermediate in both roof extent and temporal emargination. In *C. reimanni* the frontal enters the temporal emargination border, in *C. novaeguineae* and the other species it does not. The height of the supraoccipital crest above the foramen magnum is extremely high in *C. reimanni,* high in *C. novaeguineae,* low in *C. longicollis,* and intermediate in *C. pritchardi.* The volume of the temporal fossa (occupied by the mandibular adductor muscle mass) is extremely large in *C. reimanni,* large in *C. novaeguineae,* smaller in *C. longicollis,* and intermediate in *C. pritchardi.*

The lateral view of the skull reveals that the relative positions of the postorbital wall strut and of the anterior edge of the brain case differ in the four species. In *C. reimanni* and *C. novaeguineae* the postorbital wall is relatively caudad and overlaps the anterior brain case, giving increased stability and strength to the anterior third of the skull. In *C. longicollis* the postorbital wall is further cephalad, making it possible to look directly through the skull between the wall and the anterior brain case, and providing less strength and stability to the anterior skull. In *C. pritchardi* this relationship of the postorbital wall and the anterior edge of the brain case is intermediate.

All four species share the following skull osteological characteristics typical of other *Chelodina*: frontals fused, prefrontals separated by frontals, nasals present, dentaries sutured, splenials present, exoccipital contact above foramen magnum, temporal arch absent, and chelid foramen absent (variably present in rudimentary form in *C. longicollis*) (see McDowell, 1983; this "chelid foramen" is also called the posterior pterygoid foramen by Legler, personal communication).

Most of the differences in skull osteology reflect the increased robusticity of the skulls in *C. novaeguineae* and *C. reimanni,* with *C. longicollis* being the least robust, and *C. pritchardi* being intermediate. These differences can be calculated and demonstrated graphically as a Robusticity Index (RI; see Fig. 13). This Index reflects the cumulative effects of increased triturating surface width, overall tympanic skull width, and skull depth for adductor muscle volume, and is determined by the formula that follows.

$$\mathrm{RI} = \frac{\mathrm{TW} \times \mathrm{SWT} \times \mathrm{SD}}{\mathrm{SL}}$$

In this formula, TW = maxillary triturating surface width, SWT = tympanic skull width, SD = midline skull depth, and SL = skull length. The Robusticity Index increases ontogenetically with size and age, and is significantly different in the four species. Increased robusticity is directly related to the increased width of the maxillary and mandibular triturating surfaces and accompanying skeletal modifications of the skulls. These modifications reflect the secondary requirements for increased posterior skull bracing resistance and increased muscular mass to allow for increased mandibular muscle adductor force generation. These skeletal modifications have also created heavier and more massive skulls in the more robust species, which can additionally be demonstrated through an analysis of relative skull and mandible mass (grams per mm skull length) versus carapace length (Fig. 14), where *C. novaeguineae* and *C. reimanni* have heavier skulls than *C. longicollis,* and *C. pritchardi* is once again intermediate.

Based on skull osteology, *C. reimanni* and *C. novaeguineae* are probably dependent on a molluscifom and gastropod diet requiring extensive crushing of hard food matter. The diets of *C. longicollis* and *C. pritchardi* are probably more generalized carnivorous or piscivorous, with less dependence on hard-shelled bivalves and snails.

Some differences were noted between skulls of New Guinean versus Australian *C. novaeguineae.* However, full analysis of external morphological differences was not undertaken, and only a few Australian specimens were available for complete study. It is premature to evaluate whether these populations are distinct or not, and they are treated here as conspecific.

Cervical Spine. Central cervical articulation pattern is (2(3(4(5)6)7(8) in 5 specimens (4 by direct exam, 1 by X-ray), the only known pattern for all Chelidae as described by Williams (1950). Atlanto-axial (C1 and C2) cervical morphology is identical in all four species: *C. pritchardi, C. novaeguineae, C. reimanni,* and *C. longicollis.*

Shell. No neural bones in 7 specimens, all pleurals meeting in the midline. Axillary buttress moderately robust, articulating with lateral first pleural and posterior third peripheral, inguinal buttress less robust, articulating with postero-lateral edge of fourth and antero-lateral edge of fifth pleurals, and anterior seventh peripheral. Suprapygal relatively wide, contacting tenth peripheral. One specimen with atypical ten peripherals on each side, rather than normal eleven. Broad contact between first peripherals and first pleurals.

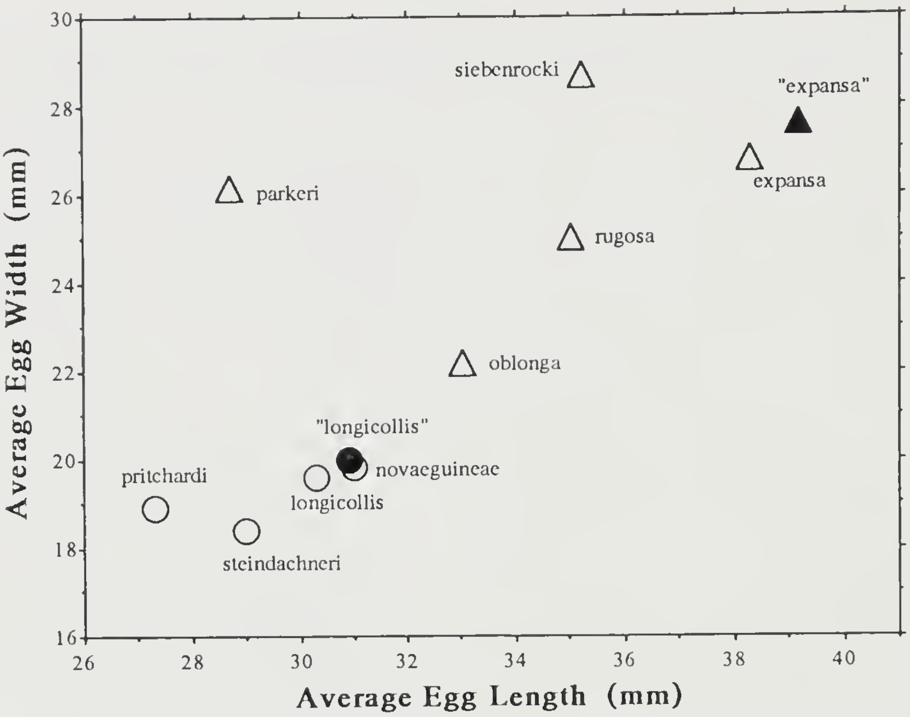

Figure 15. Plot of average egg width versus average egg length in all species of *Chelodina.* Circles represent subgeneric group "A" species; triangles, subgeneric group "B" species. Solid symbols are Legler's (1985) composite groups. See Table 5 for supporting data.

Ecology and General

Reproduction. Two specimens, obtained from Hula, each had eggs. The larger female (CL 228 mm) laid 4 eggs in captivity in Florida, one was broken, the other three measured 27.9 × 19.2, 27.8 × 18.0, and 27.0 × 18.6 mm. The smaller female (CL 193 mm) had one shelled oviducal egg measuring 26.4 × 19.7 mm when dissected post-mortem. All eggs were white, oval, with hard, brittle shells. Eggs are smaller than any other species of *Chelodina* (Table 5 and Fig. 15), but similar in shape to most other *Chelodina* (Fig. 16). Compared to the size of the adult female, the eggs laid by *C. pritchardi* are proportionately extremely small (Fig. 17).

Growth. The sub-adult male holotype has prominent concentric wide growth zones evident on carapacial and plastral scutes indicating rapid juvenile growth. No larger adults noted with similar growth evidence.

Sympatry. Chelodina pritchardi occurs sympatrically with *Emydura subglobosa* in the Kemp Welch River drainage basin. Both of these species are commonly eaten by the local inhabitants

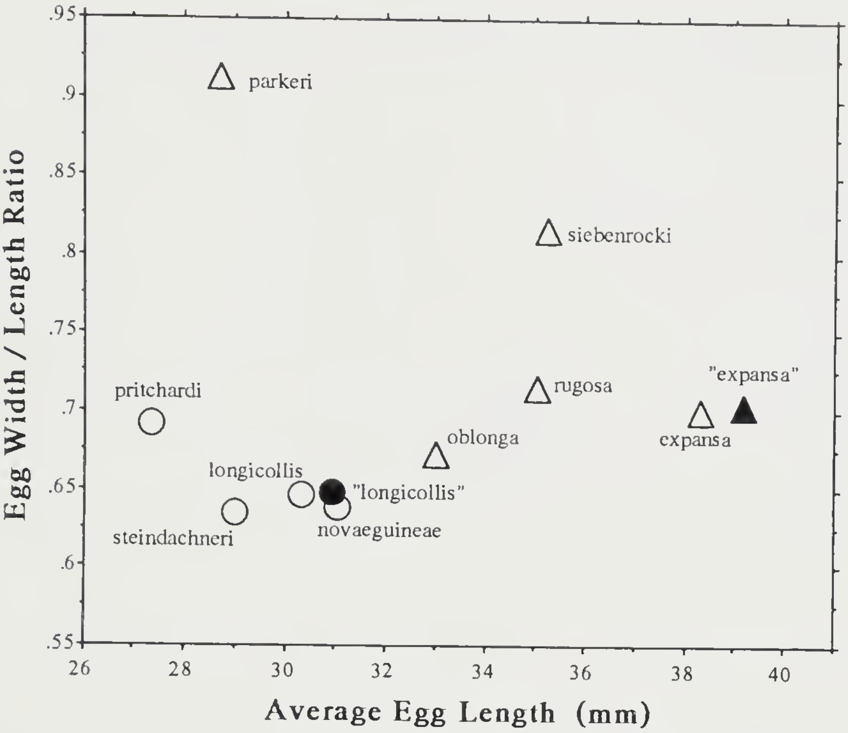

Figure 16. Plot of egg width/length ratio versus average egg length in all species of *Chelodina*. Circles represent subgeneric group "A" species; triangles, subgeneric group "B" species. Solid symbols are Legler's (1985) composite groups. See Table 5 for supporting data.

and often kept in the villages. The giant softshell turtle *Pelochelys bibroni* occurs in the Laloki River in the Port Moresby region and may be sympatric with *C. pritchardi,* which has tentatively been recorded from the same area.

Vernacular Names. In the inland regions of the Kemp Welch River area, the local language is Sinaugoro (Guise, 1985). All freshwater turtles are known as *gaokori,* but *C. pritchardi* and *E. subglobosa* do not have different names, despite the fact that the villagers readily distinguished them as being different. The Sinaugoro name for marine turtles is *gaogao.* In the coastal regions the local language is Keapara (Guise, 1985) and only one vernacular name, *aoao,* refers to both marine and freshwater swamp turtles (see also Rhodin *et al.,* 1980).

DISCUSSION

Chelodina pritchardi is in most ways more closely related to its geographically distant Australian congener *C. longicollis* than it is to the more geographically proximate New Guinean *C. novae-*

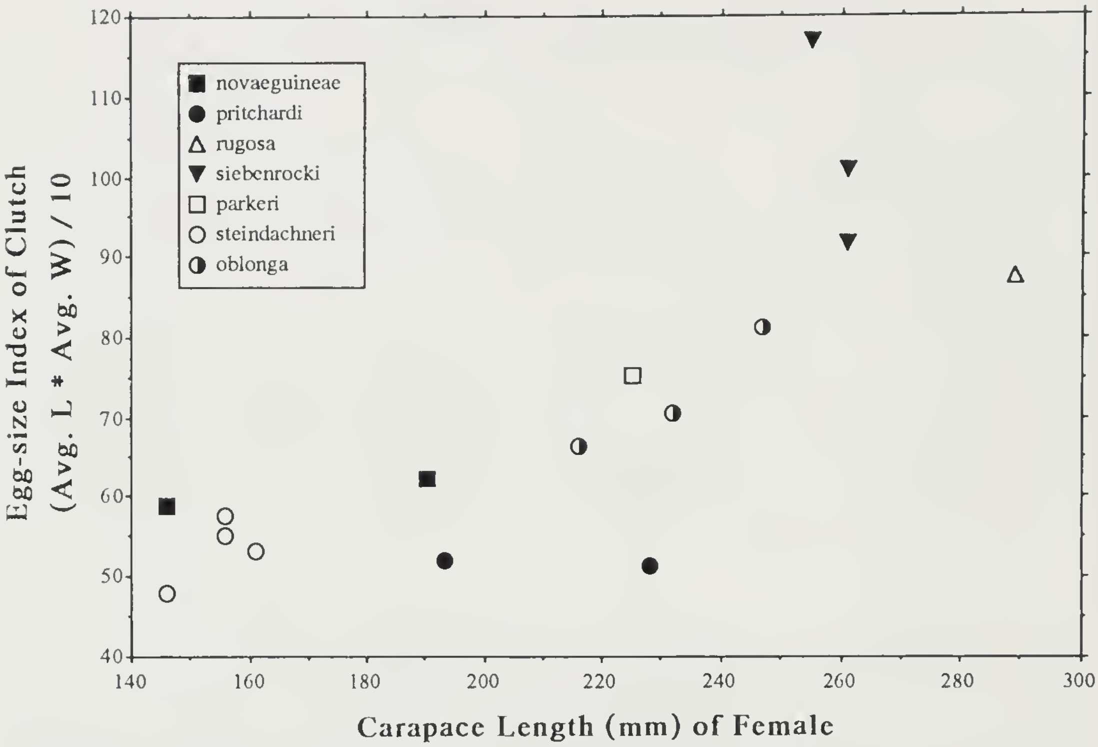

Figure 17. Plot of egg-size index of individual clutches (avg. egg length × avg. egg width/10) versus carapace length of female that laid the clutch. Smaller index indicates smaller eggs. Data based on information from sources in Table 5. Note that for its body size, *C. pritchardi* has eggs relatively smaller than the other taxa.

guineae or *C. reimanni.* A number of shared osteological features of the skull suggest a close phylogenetic relationship between *C. pritchardi* and *C. longicollis,* and I regard them as more closely related to each other than either is to any other species. Superficially, however, based on only external morphology, *C. pritchardi* appears more similar to *C. novaeguineae* than to *C. longicollis.*

Chelodina novaeguineae is more similar to *C. pritchardi* than it is to *C. longicollis,* but its most closely related congener is *C. reimanni.* This latter species was described in 1990 by Philippen and Grossman, but they failed to describe the osteology or to compare their species to other New Guinean or Australian *Chelodina.* I have had an opportunity to examine several specimens of *C. reimanni,* including two osteological preparations (AGJR-T 746, a female of 199 mm carapace length from Merauke, Irian Jaya obtained via Michael Reimann and Walter Sachsse, and AGJR-T 1614, a female of 170.5 mm carapace length from Mer-

Table 5. Average length and width of eggs for various species of *Chelodina*. CL_{Max} = maximum carapace length (mm). Values: mean ± standard deviation (range) (mm). *Chelodina* "*longicollis*" and "*expansa*" (in quotations) are the subgeneric groupings of Legler, where he combines data from several different species.

Species	CL_{Max}	$Eggs_n$	Length	Width	Reference
C. pritchardi	228	4	27.3 ± 0.71 (26.4–27.9)	18.9 ± 0.74 (18.0–19.7)	Present study
C. novaeguineae	218	12	31.0 ± 1.08 (29.2–32.3)	19.8 ± 0.86 (18.5–20.9)	Present study
C. siebenrocki	290	64	35.2 ± 1.70 (31.6–38.3)	28.7 ± 1.10 (27.2–31.7)	Rhodin and McCord, 1990; Rhodin and Mittermeier, 1976
C. parkeri	267	13	28.7 ± 3.20 (25.5–32.0)	26.2 ± 0.80 (24.0–27.0)	Ewert, 1985; Fritz and Jauch, 1989
C. oblonga	247	80	33.0 ± 1.30 (30.8–35.7)	22.2 ± 1.57 (18.1–24.0)	Clay, 1981; Kuchling, 1988
C. rugosa	304	14	35.0	25.0	Cann, 1978
C. expansa	375	46	38.3 ± 0.30 (33.5–41.9)	26.8 ± 0.40 (22.2–30.1)	Georges, 1986
C. "*expansa*"	375	304	39.2 ± 3.40 (30.7–46.9)	27.6 ± 2.41 (19.5–31.0)	Legler, 1985
C. steindachneri	193	30	29.0 ± 0.94 (27.5–31.0)	18.4 ± 0.80 (17.0–19.5)	Kuchling, 1988
C. longicollis	240	154	30.3 ± 0.83 (21.0–33.8)	19.6 ± 0.27 (12.5–21.3)	Vestjens, 1969; Legler and Cann, 1980
C. longicollis	240	169	31.2 ± 0.1	20.2 ± 0.1	Palmer-Allen *et al.*, 1991
C. "*longicollis*"	279	282	30.9 ± 2.88 (20.2–42.5)	20.0 ± 1.86 (15.8–29.1)	Legler, 1985

auke obtained via Frank Yowono and William McCord). *Chelodina reimanni* is most similar to *C. novaeguineae* and the features of increased skull robusticity seen in *C. novaeguineae* are further amplified in *C. reimanni.* Its skull is massively enlarged and heavy, with wide triturating surfaces, a narrow parietal crest, large temporal fossa, and increased buttressing in a deep, wide skull. It has small fused premaxillas and lacks chelid foramina. I regard *C. novaeguineae* and *C. reimanni* as more closely related to each other than either is to any other species, and from my preliminary examination, I also recognize *C. reimanni* as being distinct from *C. novaeguineae.*

Phylogenetically, I consider enlarged maxillary and mandibular triturating surfaces and increased skull robusticity as derived features within the *Chelodina* lineage. Though clearly diet-related, these features represent a significant specialization by only a few members of the genus, notably *C. reimanni* and *C. novaeguineae.* These shared derived characteristics suggest a close phylogenetic relationship between these two species. The narrow triturating surfaces and less robust skulls of *C. pritchardi* and *C. longicollis* represent more primitive features within the genus and suggest retained plesiomorphic features in those two species. These primitive features are also present in the only other member of *Chelodina* subgeneric group "A", the western Australian species *C. steindachneri.* Examination of skulls of this species demonstrates that it is most similar to *C. longicollis,* with narrow triturating surfaces, a relatively wide anterior parietal roof, shallow temporal fossa, and markedly decreased skull robusticity. Unlike *C. longicollis,* however, it usually retains fairly well-formed chelid foramina (posterior pterygoid foramen of Legler), a relatively primitive feature among all *Chelodina.* The chelid foramen is absent in all other members of *Chelodina* subgeneric groups "B" and "A" except for *C. longicollis,* where it is variably present but usually absent.

Of the five currently recognized taxa in *Chelodina* subgeneric group "A", I regard *C. reimanni* as the most derived, and *C. steindachneri* as the most primitive. The other three species fall out in a series between these extremes, with *C. novaeguineae* most derived, *C. longicollis* most primitive, and *C. pritchardi* intermediate between the two. Two alternate phylogenetic hypotheses

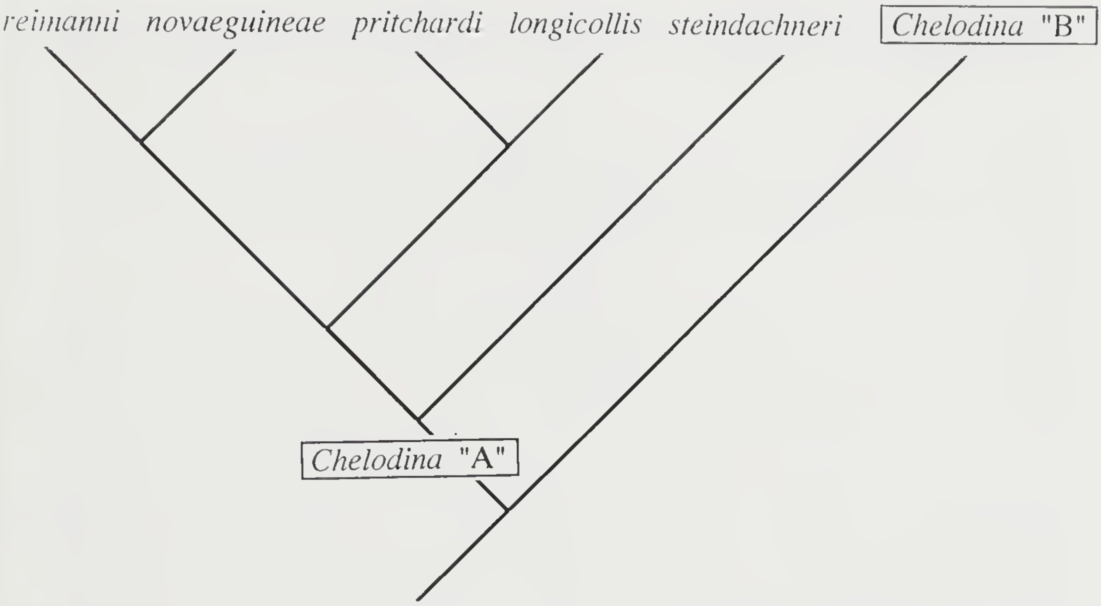
reimanni
novaeguineae
pritchardi
longicollis
steindachneri
Chelodina "B"
Chelodina "A"

Figure 18. Hypothesized relationships of the currently recognized species of *Chelodina* subgeneric group "A". See Figure 19 for an alternative phylogenetic hypothesis.

expressing the possible relationships within *Chelodina* subgeneric group "A" are depicted in Figures 18 and 19, with Figure 18 representing what I consider the more likely hypothesis. This hypothesis would be strengthened through the discovery of shared

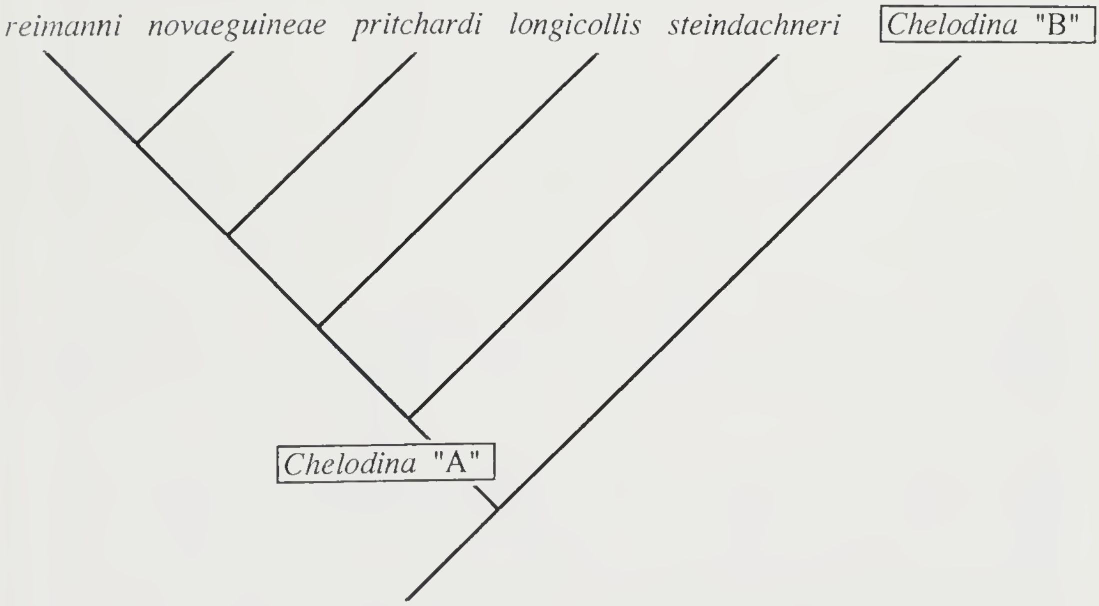
reimanni
novaeguineae
pritchardi
longicollis
steindachneri
Chelodina "B"
Chelodina "A"

Figure 19. Alternative phylogenetic relationships of *Chelodina* subgeneric group "A". See Figure 11 for preferred hypothesis.

derived features between *C. pritchardi* and *C. longicollis,* and is encumbered by the less parsimonious double loss of chelid foramina in the *novaeguineae-reimanni* lineage and the *pritchardi-longicollis* clade. Clearly, a rigorous cladistic analysis of multiple morphologic features of all the species of *Chelodina* will be necessary to help further elucidate the phylogenetic history of the genus.

These five taxa of *Chelodina* subgeneric group "A" form a well-defined monophyletic assemblage clearly differentiated from *Chelodina* subgeneric group "B". Features of shell morphology, head width, skull osteology, and cervical spine length and morphology clearly define the two groups. The currently recognized genus *Chelodina* (sensu lato) is also a clearly defined monophyletic assemblage with a long list of shared derived characteristics (see Gaffney, 1977). Recognition of this monophyly needs to be incorporated into whatever taxonomic arrangement provides the most specific nomenclatorial definition of the subgroups involved. Whether the "subgeneric" groups "A" and "B" are best recognized as subgenera of *Chelodina* or as full separate genera awaits full evaluation by Legler (in preparation). My own analysis of the phylogenetic relationships of all the Chelidae of Australasia and South America (in preparation) suggests recognition at the generic level for these two separate groups of *Chelodina,* with a new suprageneric category replacing our old concept of *Chelodina.*

ACKNOWLEDGMENTS

I thank Peter C. H. Pritchard for his donation of the two specimens which stimulated this study and William P. McCord for his generosity in allowing me to examine and measure his large series of live captive animals. I also thank Richard Zweifel, opportunely present in Papua New Guinea when I collected the holotype, for facilitating export of the specimen via the American Museum of Natural History to the MCZ. Susan and Michael Rhodin provided valuable field assistance and José Rosado at the MCZ curated specimens and helped with logistics. I prepared all illustrations. For the loan of other study specimens and general assistance with the project, I also thank John Legler, Robert Winokur, Arnold Kluge, Allen Greer, Ron Heyer, Sam McDowell, Alan Leviton, A. F. Stimson, Philip Hall, Walter Sachsse, Chuck

Crumly, John Iverson, John Carr, Russ Mittermeier, and Ernest Williams.

APPENDIX

Comparative material examined; collection acronyms as follows: AGJR-T = personal collection of Rhodin (including preserved specimens, voucher photographs, and reliably documented database entries, including data from many live specimens measured in the unnumbered personal collection of William P. McCord); AMNH = American Museum of Natural History; AMS = Australian Museum, Sydney; BMNH = British Museum of Natural History; CAS = California Academy of Sciences; FMNH = Field Museum of Natural History; MCZ = Museum of Comparative Zoology; MTKD = Museum für Tierkunde, Dresden; PCHP = personal collection of Peter C. H. Pritchard; PNGM = Papua New Guinea Museum; SMcD = collection of Samuel McDowell; UMMZ = University of Michigan Museum of Zoology; UNLV = University of Nevada, Las Vegas; USNM = United States National Museum; UU = University of Utah.

Chelodina longicollis: **Australia:** *New South Wales:* Armidale (nr.), UNLV s/n (15); Sydney, AMNH 14151; Sydney, 60 mi S, UMMZ 130161, 130549; Talbnager R., 8 mi W Varbry, btw. Dunedo and Cassilis, AMS 40828; *Victoria:* Bright, FMNH 75317; Patho, 5 mi S Murray R., 20 mi W Echuca, UU s/n, AMNH 108952, *Queensland:* Burnett R., FMNH 16885; Capella, 20 mi W, CAS 77809; Duaringa, 15 mi S, CAS 77808; Eidsvold, upper Burnett River, AMS 5979; *No data:* AMNH s/n (2), UU s/n, AGJR-T 133, 158-9, 179, AMNH 2323, MCZ 8369, 8371-7, 86783-4, USNM 8894, AMNH 9002, 45079, 45085, 75165, 97629, 110483, MTKD 14605, FMNH 22681, 31047, 35538, BMNH 1947.3.5.86 (holotype of *C. longicollis*), BMNH 1947.3.5.87 (holotype of *C. sulcata*).

Chelodina novaeguineae: **Australia:** *Queensland:* Alice River, 15 mi WSW Townsville, UMMZ 132328; Armraynald, 26 mi SE Burketown, AMNH 86545-7, Burdekin River, lower, BMNH 1908.2.25.1; Edward River, Cape York, UU 14718; Greta Creek, PCHP 2385; Staaten R., 100 mi. N Normanton, AMNH 86543-4; *Northern Territory:* Batten Creek, 13 mi WSW Borroloola, UU 14716; **Indonesia:** *Irian Jaya:* Kuprik, nr. Merauke (8°25'S, 140°28'E), SMcD 49-1, 49-2; **Papua New Guinea:** *Western Province:* Abam, Oriomo R. (8°57'S, 143°13'E), AMNH 117939, MCZ 120353, 127404, 134390-1, 134709-10, 134712; Ali Village, Aramia River (8°05'S, 142°55'E), USNM 213490; Boze, Binaturi River (9°05'S, 143°01'E), AGJR-T 504; Daru Roads (9°03'S, 143°12'E), MCZ 142500; Emeti, Bamu River (7°48'S, 143°15'E), MCZ 138102; Fly River at Strickland River junction (7°35'S, 141°25'E), MCZ 53758-61; Giringarede, Binaturi River (9°03'S, 142°57'E), MCZ 153930; Katatai (9°01'S, 143°18'E), MCZ 138101, 142495, 154340;

Katow (= Mawatta, Binaturi River) (9°08′S, 142°55′E), BMNH 1946.1.22.36 (lectotype *C. novaeguineae*); Komovai Village, Fly River (7°33′S, 141°15′E) AGJR-T 1338; Kuru, Binaturi River (8°55′S, 143°04′E), MCZ 134711; Lake Daviumbo (7°35′S, 141°17′E), AMNH 59874; Lake Murray (7°00′S, 141°30′E), MCZ 134392; Mabaduane, Pahoturi River (9°17′S, 142°44′E), AMNH 57589-91, MCZ 137516; Masingle, Binaturi River (9°07′S, 142°55′E), AGJR-T 501, MCZ 153046-8, 153906, 153923, 153926; Morehead (8°43′S, 141°38′E), PNGM 23505; No data, USNM 231527; Oriomo, Oriomo River (8°52′S, 143°10′E), PNGM 23510; Peawa, Oriomo River (8°55′S, 143°12′E), AMNH 104010; Tarara, Wassikussa River (8°50′S, 141°52′E), AMNH 58410; Togo, Pahoturi River (9°14′S, 142°40′E), PNGM 23502-3, 23511, MCZ 134393-6; Ume, Binaturi River (9°03′S, 143°03E), PNGM 22407, MCZ 127405; Wipim (8°51′S, 142°55′E), USNM 204856.

Chelodina pritchardi: **Papua New Guinea:** *Central Province:* Bore, Kemp Welch River (9°53′S, 147°46′E), MCZ 173543; nr. Hula, Kemp Welch River basin (10°06′S, 147°43′E), MCZ 175813, AMNH 139735; nr. Port Moresby, PNGM 23373; ca. 10 km east of Bore, Kemp Welch River, AGJR-T 1575-1609, 1643-6.

Chelodina reimanni: **Indonesia:** *Irian Jaya:* Merauke (8°25′S, 140°28′E), AGJR-T 746, 1299-1300, 1325, 1614-1619, 1642; *No data:* MTKD 14603.

Chelodina steindachneri: **Australia:** *Western Australia:* Marloo Station, MCZ 33501; Mundabullangana, MCZ 74871, 134469; 1 mi S. Minilya River on NW coastal hwy., MCZ 74872; Woodstock, AMNH 101977-9.

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CHELID TURTLES OF THE AUSTRALASIAN ARCHIPELAGO: II. A NEW SPECIES OF *CHELODINA* FROM ROTI ISLAND, INDONESIA

ANDERS G. J. RHODIN[1]

ABSTRACT. A new species of *Chelodina* (Testudines: Pleurodira: Chelidae) is described from Roti Island, west of Timor, East Nusa Tenggara Province, in the southeastern Indonesian Archipelago. The species is endemic to Roti, a small and relatively xeric island. It is most similar and most closely related to *Chelodina pritchardi* from Papua New Guinea and *C. longicollis* from Australia, less closely related to *C. novaeguineae* and *C. reimanni* from New Guinea.

INTRODUCTION

The side-necked turtles of the family Chelidae that inhabit the Australasian Archipelago of eastern Indonesia and Papua New Guinea remain one of the least well known turtle faunas of the world. Until recently only two species of the snake-necked genus *Chelodina* were known from the regions north of Australia: *Chelodina novaeguineae* Boulenger, 1888 and *Chelodina siebenrocki* Werner, 1901. Since 1975, systematic studies have revealed an additional three species: *Chelodina parkeri* Rhodin and Mittermeier, 1976, *Chelodina reimanni* Philippen and Grossman, 1990, and *Chelodina pritchardi* Rhodin, 1993. The last of these, from the Kemp Welch River of southeastern Papua New Guinea, was described in the first paper of this series on the chelid turtles of the Australasian Archipelago. In this second paper of the series, I describe another new species of *Chelodina,* this time from Roti Island, west of Timor in southeastern Indonesia.

The first species of *Chelodina* to be described from anywhere in the Australasian Archipelago was *C. novaeguineae* Boulenger,

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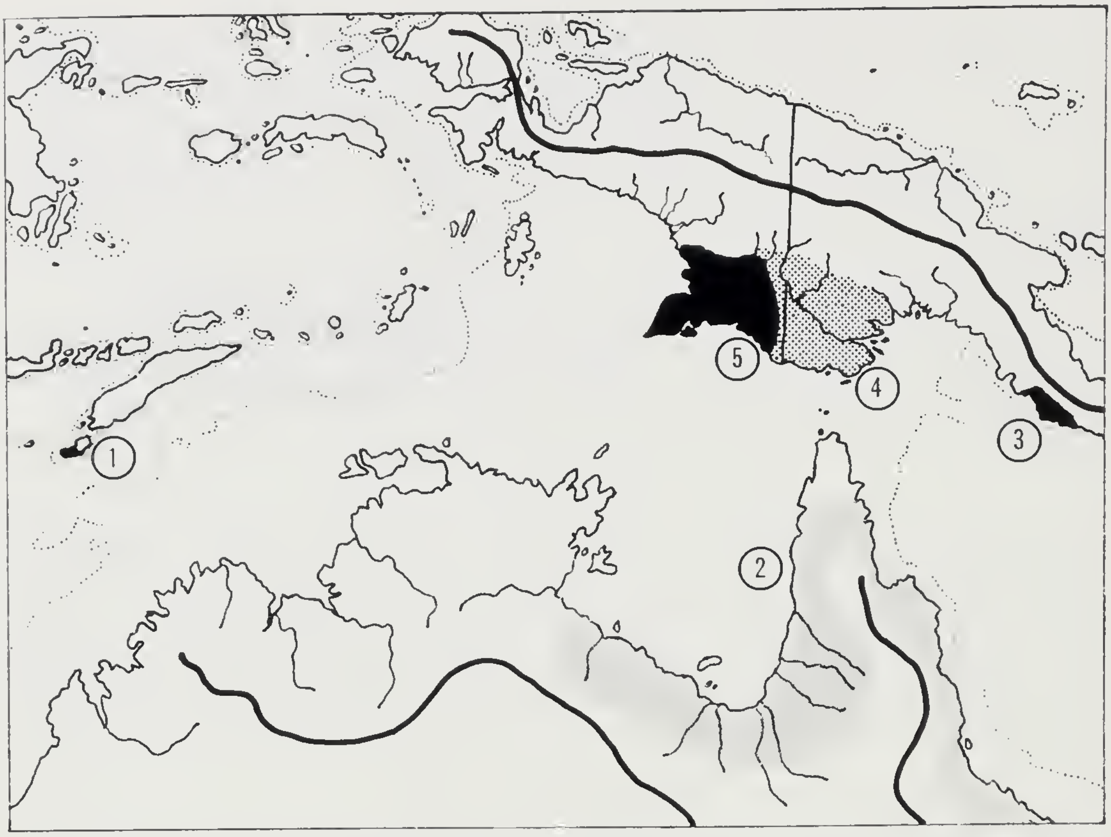

Figure 1. Distribution of *Chelodina* subgeneric group "A" in northern Australia, New Guinea, and southeastern Indonesia. 1. Distribution of *Chelodina mccordi* on southwestern Roti Island, Indonesia. 2. Australian distribution of *C. novaeguineae* (sensu lato) in Northern Territory and Queensland. 3. Distribution of *C. pritchardi* in Papua New Guinea. 4. New Guinean distribution of *C. novaeguineae* in Irian Jaya and Papua New Guinea. 5. Approximate distribution of *C. reimanni* in Irian Jaya, Indonesia. Major watershed limits in New Guinea and Australia indicated as thick lines; thin dotted lines mark the 200 meter water depth limits around the eastern Indonesian islands as well as the continental Sahul Shelf surrounding Australia and New Guinea.

1888, which came from the southern New Guinea coastal region of what is now designated as the Western Province of Papua New Guinea. It is distributed throughout southern lowland New Guinea including extreme southeastern Indonesian Irian Jaya and southwestern Papua New Guinea. Similar forms of *Chelodina novaeguineae* (sensu lato) also occur in northern Queensland and northeastern Northern Territory in Australia (Fig. 1), although these forms probably represent separate and distinct taxa (J. Cann, personal communication to W. P. McCord). Soon after the original description of *C. novaeguineae,* Lidth de Jeude (1895) described three specimens of this species from the island of Roti (originally spelled "Rotti"), west of Timor in southeastern present-day Indonesia. These specimens were collected on Roti in 1891 by Dr. Herman F. C. Ten Kate and donated to the Leiden Museum. Though extremely isolated from the rest of the range of *C. novaeguineae,* this locality has subsequently been duly noted in the distribution of *C. novaeguineae* without any further attempts at critical systematic comparison of its population to the populations in the New Guinean and Australian portions of the range. From the zoogeographic isolation of Roti, I long suspected that this population, if natural, must certainly represent a separate and distinct species, though probably closely related to *C. novaeguineae* (sensu stricto).

Unfortunately, Roti has become a difficult place to visit for field studies, due in part to the political upheaval on neighboring Timor, associated with the recent incorporation of Portuguese East Timor into Indonesia. For many years I attempted unsuccessfully to travel to Roti. A few years ago, I was fortunate to meet Dr. William P. McCord, who maintains an enormous collection of live turtles and whose primary interest is the diversity of species in the genus *Chelodina.* Dr. McCord, through his collection contacts in Indonesia (notably Mr. Frank Yowono), had recently succeeded in obtaining a series of 16 *Chelodina* from Roti. When I examined them, my original conviction that the Roti animals would be different from mainland New Guinean and Australian *C. novaeguineae* was confirmed.

Subsequent to my analysis of the McCord collection of Roti animals I obtained on loan two of the original specimens collected in 1891 by Dr. Ten Kate on Roti and still present in the National Museum of Natural History in Leiden. A comparison of those specimens with the description by Lidth de Jeude (1895) confirms that they are the original specimens, and that they are also the same taxon as McCord's specimens obtained from Roti by Frank Yowono. Both Leiden specimens also bear tags with the manuscript name "*Chelodina rottiensis* Brongersma." This name must now be considered a nomen nudum, as it was never published or described, but clearly Dr. Brongersma also deserves mention and credit for having previously recognized the distinctiveness of this new taxon from Roti. I thank him and Dr. Hoogmoed for releasing the specimens and relinquishing claims to the formal description.

These 18 specimens of *Chelodina* from Roti Island were then critically compared to a series of 43 *Chelodina pritchardi* from southeastern Papua New Guinea, 51 *C. novaeguineae* from southwestern Papua New Guinea and adjacent Irian Jaya, 10 *C. novaeguineae* from northern Australia, 54 *C. longicollis* from eastern Australia, 12 *C. reimanni* from southeastern Irian Jaya, Indonesia, and 7 *C. steindachneri* from western Australia, for a total study series of 195 specimens. Analysis of external morphology and cranial osteology demonstrated that this isolated Roti population of *Chelodina* is indeed a new and distinct species of *Chelodina* subgeneric group "A" (sensu Goode, 1967). It is more similar to *C. pritchardi* of Papua New Guinea than it is to either New Guinean or Australian populations of *C. novaeguineae.* It now gives me great pleasure to formally describe this new species of *Chelodina* and to name it in honor of Dr. William P. McCord who succeeded in obtaining the series of animals that made confirmation and description of the new species possible.

TAXONOMY

Chelodina mccordi, sp. nov.

(Figs. 2–5)

Chelodina novae guineae (partim) Ten Kate, 1894:689
Chelodina novae-guineae (partim) Lidth de Jeude, 1895:119; De Rooij, 1915:315

Holotype. MCZ 176730 (Fig. 2), alcohol-preserved adult female of 197.5 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island, East Nusa Tenggara Province, Indonesia; specimen is formerly from the private live collection of William P. McCord, and also bears old tag AGJR 450 from the personal preserved collection of Rhodin.

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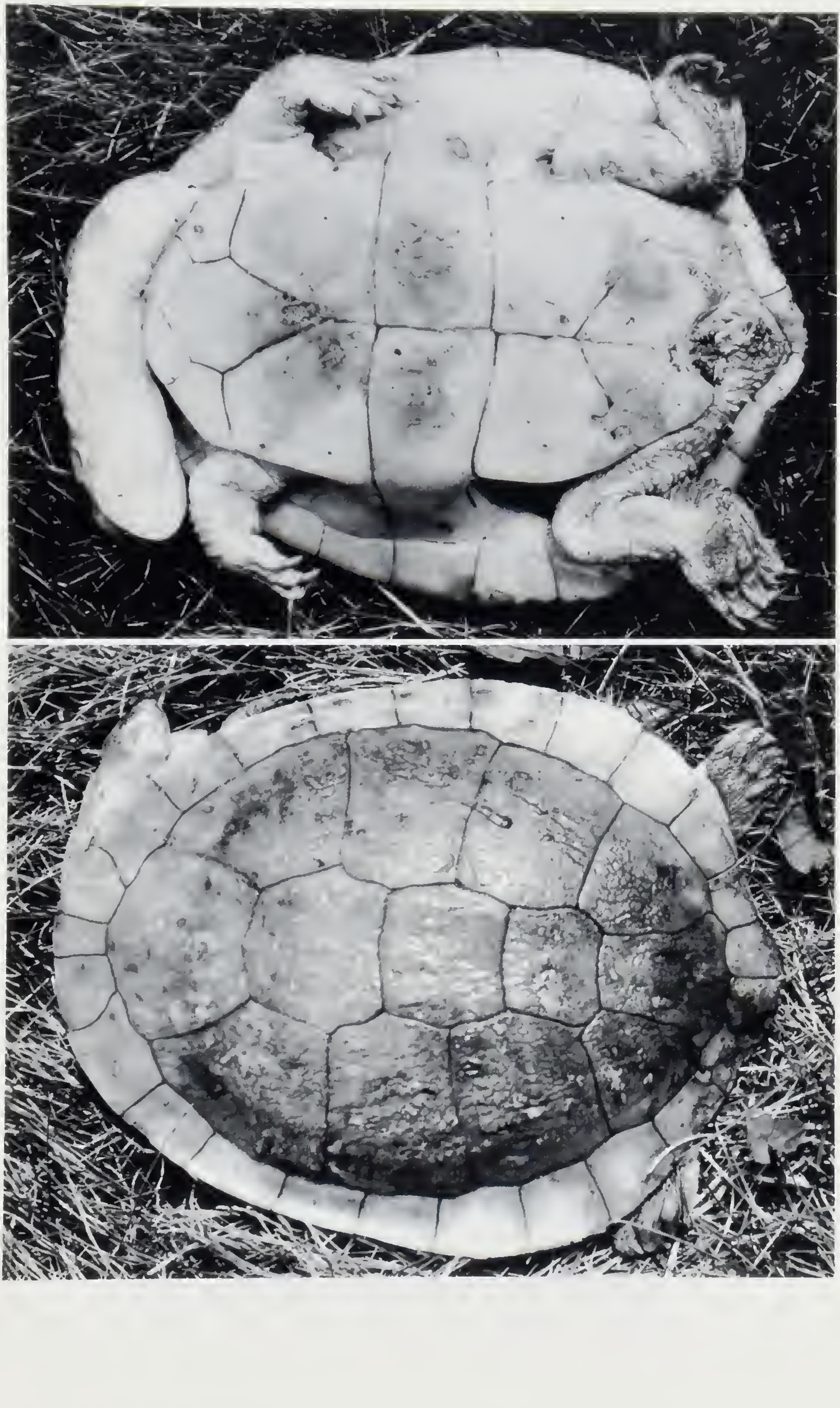
Figure 2. Holotype of *Chelodina mccordi* (MCZ 176730), adult female measuring 197.5 mm carapace length, from Roti Island, Indonesia.



Paratypes. MCZ 176731, alcohol-preserved adult male of 153 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island; specimen is formerly from the private live collection of William P. McCord, and also bears old tag AGJR 364 from the personal preserved collection of Rhodin; MCZ 176732 (Fig. 3), alcohol-preserved adult female of 194 mm carapace length, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island; specimen is formerly from the private collection of William P. McCord, and also bears old tag AGJR 368 from the private preserved collection of Rhodin; RMNH 10187 (Figs. 4–5), skeletal preparation of shell, skull, and limbs of adult of unknown sex (but probably female) of 179.5 mm carapace length, collected by Dr. Herman F. C. Ten Kate on "Rotti" [Roti Island, Indonesia] in 1891, originally described by Lidth de Jeude (1895) as a specimen of *Chelodina novaeguineae* Boulenger, 1888.

Referred Specimens. RMNH 4349, collected by Dr. Herman F. C. Ten Kate on "Rotti" [Roti Island, Indonesia] in 1891, originally described by Lidth de Jeude (1895) as a specimen of *Chelodina novaeguineae* Boulenger, 1888; AGJR 365–7, 369, 448–9, 452–7, 460, purchased from native villagers by Frank Yowono in Kupang, western Timor, originally collected on Roti Island, Indonesia, and formerly from the private live collection of William P. McCord. Personal specimens available on loan through the Chelonian Research Foundation, and eventually to be deposited at the Museum of Comparative Zoology.

Distribution. Known only from Roti Island, located about 20 km southwest of the western end of Timor in the Lesser Sunda Islands in the Province of East Nusa Tenggara of the southeastern Indonesian Archipelago (Fig. 1). Not known to occur on Timor itself. No current localities on Roti Island precisely documented as yet, but collectors indicate that the species is most readily found in rice paddies. Most rice paddies are located in the southwestern half of the island west and north of the village of Tudameda, and along the cross-island road between Tudameda and Ba'a. In addition, there are some limited rice paddies and small lakes in the northeast peninsular region of the island where the species might also occur, but a large portion of the rest of the island is relatively

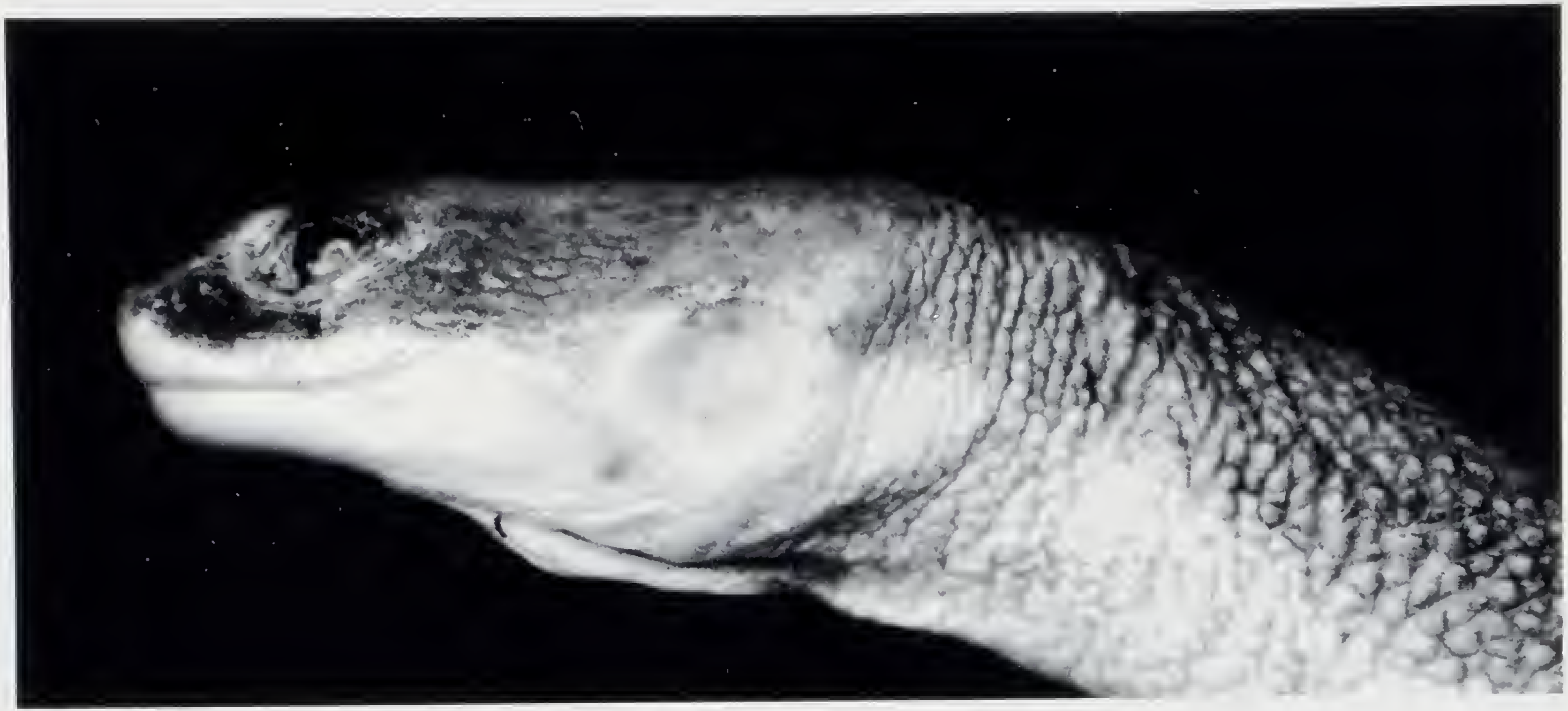


Figure 3. Lateral head view of *Chelodina mccordi* (Paratype MCZ 176732), adult female.

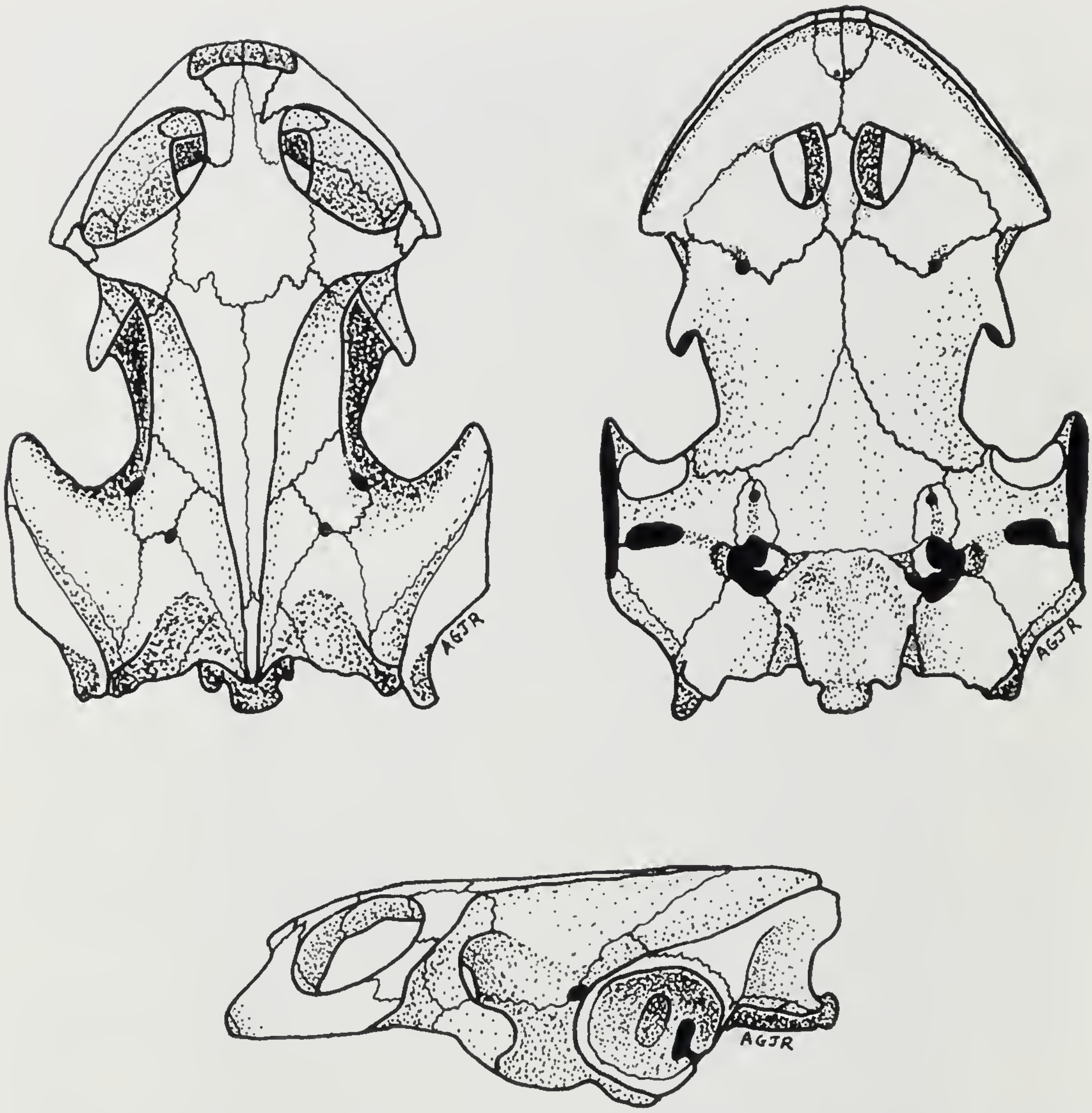


Figure 4. Dorsal, ventral, and lateral views of skull of *Chelodina mccordi* (Paratype RMNH 10187, adult of unknown sex measuring 179.5 mm carapace length) from Roti Island, Indonesia.

xeric with little surface water. The total area of Roti Island is only about 1,214 km^2, while the highest elevation reaches 444 m.

Type Locality. The collection locality of the holotype specimen obtained by Yowono from Roti Island cannot be stated precisely.

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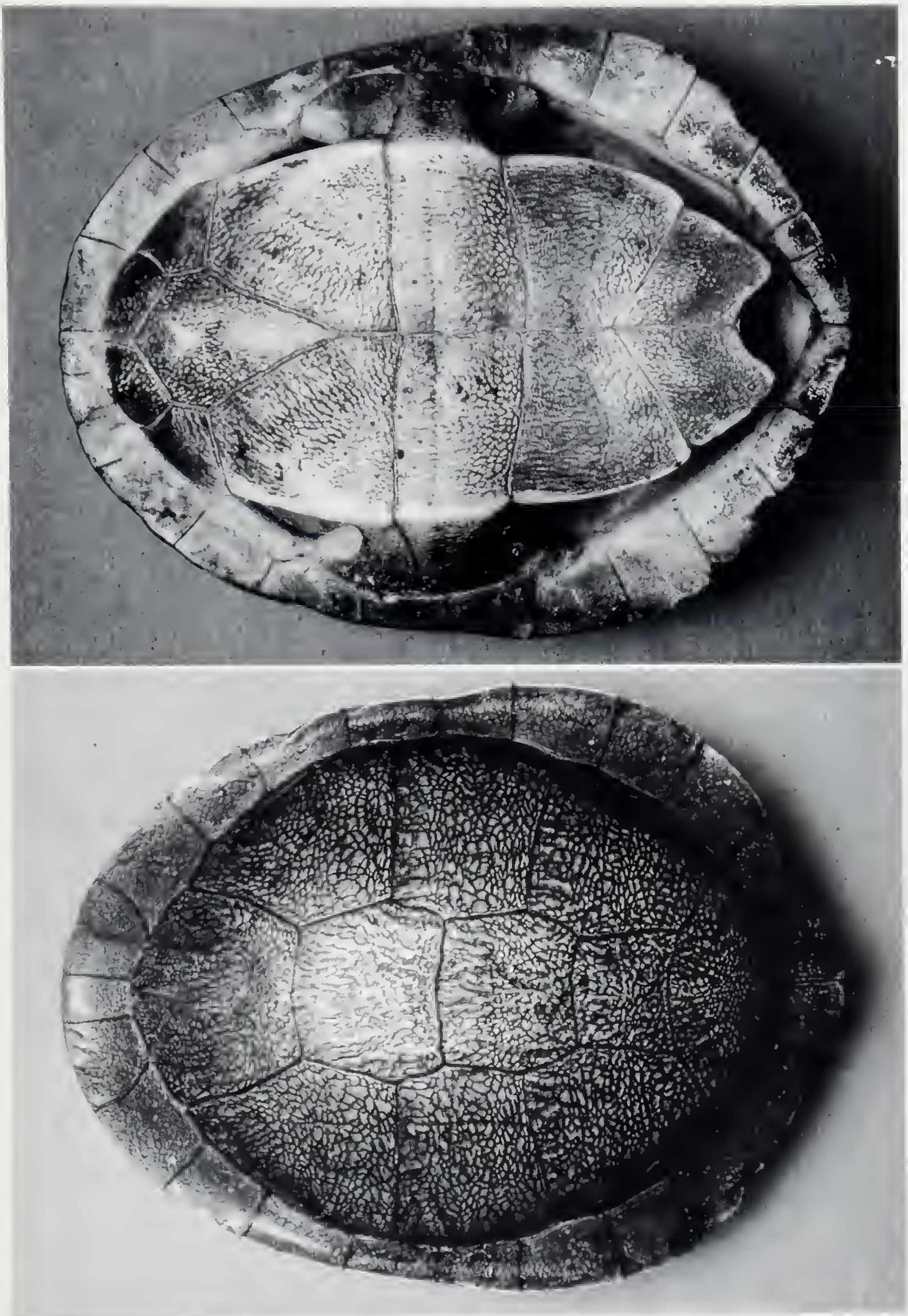
Figure 5. Shell of *Chelodina mccordi* (Paratype RMNH 10187), originally collected in southwestern Roti in 1891 by Dr. Herman F. C. Ten Kate and described by Lidth de Jeude (1895).



However, a review of the natural history and travel writings of Dr. Ten Kate, who collected three specimens in 1891, including one of the paratypes, and a careful study of older and modern maps of Roti can help further restrict the probable type locality. Dr. Ten Kate states in his travelogue (Ten Kate, 1894:688–689) that he observed a small specimen of *Chelodina novae guineae* [= *Chelodina mccordi*] that fishermen had just caught on 7 September 1891 at the inland freshwater lake "Danau Naloek (Naroek)" near lake "Danau Linggoe" [*Danau* = *Lake* in Bahasa Indonesian]. Danau Naloek was reached approximately three fifths of the way along a four and a half hour trip while Dr. Ten Kate traveled from "Ti-Kanakétoe" (also referred to as simply "Ti") [= modern Danaheo, or Danahoe, along the southwestern shore, 4 km south of Tudameda] to "Baä" [= modern Ba'a along the northern shore]. The locality "Danau Naloek" does not appear on modern maps, but Dr. Ten Kate mentions that he followed Dr. Wichmann's earlier route through the area, and Wichmann (1892) shows the lake "Danu naluk" on his map about halfway between Ti and Baä, which he also indicates by their more modern names of Danoheoh and Namudale [= Namodale, a suburb of Ba'a]. Dr. Ten Kate further states that Danau Naloek was located in the middle of dry rolling grassland, and that shortly after leaving the lake he entered forested landscape at "boschrijke . . . Lóameko" where he crossed the administrative border between Dengka and Lelain. This provincial boundary still occurs on modern maps with the villages of Busalangga and Longgo [probably = Danau Linggoe] just west of there, at approximately the three fifths point along the Danaheo-Ba'a road. It is therefore reasonable to state that the species occurred at Danau Naloek in the Busalangga region in 1891 and to assume that Dr. Ten Kate probably collected or obtained at least one of his paratype specimens there. Therefore, the type locality of *Chelodina mccordi* is hereby restricted to Danau Naloek, near Busalangga, ca. 11 km northeast of Tudameda and ca. 8 km southwest of Ba'a, elevation ca. 115 m, southwestern Roti Island (10°48′S, 123°00′E), East Nusa Tenggara Province, Indonesia.

Diagnosis. A medium-sized isolated Rotinese snake-necked chelid turtle of *Chelodina* subgeneric group "A" (sensu Goode, 1967 and Burbidge *et al.,* 1974) with relatively wide head, wide

TABLE 1. FEATURES DISTINGUISHING FOUR SPECIES OF *CHELODINA* SUBGENERIC GROUP "A". FOR MERISTIC BASIS OF DISTINGUISHING FEATURES, SEE TABLES 3 AND 5 AND FIGURES 4–6. PLUSES AND MINUSES FOR THE INTERMEDIATE CATEGORIES INDICATE SLIGHT DIFFERENTIATION BETWEEN THE TWO SPECIES IN THAT CATEGORY.

Feature	*longicollis*	*pritchardi*	*mccordi*	*novaeguineae*
External				
Carapace width	Interm.	Wide	Wide	Narrow
Head width	Narrow	Narrow	Wide	Wide
Plastron width	Wide	Interm.	Narrow	Narrow
Marginal 1 width	Wide	Wide	Narrow	Interm.
Composite ratio	Low	Interm. (−)	High	Interm. (+)
Osteology				
Triturating width	Narrow	Interm. (−)	Interm. (+)	Wide
Skull depth	Shallow	Interm.	Interm.	Deep
Skull width	Narrow	Narrow	Wide	Wide
Robusticity	Low	Interm. (−)	Interm. (+)	High

carapace, narrow plastron, narrow first marginal, wide skull, intermediate triturating surface width, intermediate skull depth, and intermediate to mildly increased skull robusticity. Most similar to *C. pritchardi,* but differentiated from it by the much narrower first marginal, relatively wider second marginal, wider head, narrower plastron, wider skull, and very slightly increased skull robusticity. Also similar to *C. novaeguineae,* but differentiated from that taxon by the wider carapace, slightly narrower first marginal, significantly narrower triturating surface width, shallower skull, and significantly decreased skull robusticity.

In most morphological respects *C. mccordi* is intermediate between *C. novaeguineae* and *C. longicollis,* and most similar to *C. pritchardi,* especially in juvenile and subadult stages. See Table 1 for a summary of differences among *C. mccordi, C. pritchardi, C. longicollis,* and *C. novaeguineae.*

Etymology. The specific epithet is a patronym honoring Dr. William P. McCord, a veterinarian with a deep interest in turtles, who was instrumental in securing the large study series demonstrating the distinctiveness of the species.

Related taxa. Chelodina mccordi is most similar to the following five chelid taxa from New Guinea and Australia, all members of *Chelodina* subgeneric group "A": *Chelodina longicollis* (Shaw, 1794), *Chelodina novaeguineae* Boulenger, 1888, *Chelodina pritchardi* Rhodin, 1993, *Chelodina reimanni* Philippen and Grossman, 1990, and *Chelodina steindachneri* Siebenrock, 1914. Type localities and specimens for these species are listed in the first paper of this series (Rhodin, 1993).

DESCRIPTION

External Morphology

Carapace. Carapace of *C. mccordi* moderately rugose and broadly oval, width averaging 77.9% of length [Fig. 6(1)A], moderately wider posteriorly at about marginals 6–7, with slight expansion of marginals 6–8. Moderately prominent lateral marginal recurving from about marginal 4 through 7, often partially involving marginals 3 and 8 as well. Somewhat less prominent recurving in smaller specimens. Moderate supracaudal ridging with slight adjacent concavity of marginal 11. No vertebral knobs, keel, or ridging. Slight vertebral flattening and shallow midline furrow in larger females, smoothly convex in smaller females and males. No supracaudal notch or marginal serrations. Dorsal nuchal long and broad, not projecting anterior to carapace margin. Ventral underlap of nuchal also relatively long and broad. Vertebral 1 widest, then 2, 3, 5, and 4 in descending order of width in normal specimens. Basic external measurements of *C. mccordi* presented in Table 2, differences from *C. pritchardi, C. novaeguineae,* and *C. reimanni* presented in Table 3 and Figure 6 (parts 1 and 2).

Many individuals with altered vertebral and costal pattern with supernumerary or fused scutes. Five of 18 specimens have 6 vertebral scutes, three with a small intercalated supernumerary scute between V3 and V4, one between V2 and V3, and one between V4 and V5. Two specimens have three symmetrical costals on each side, one has three costals on one side, four on the other. This deformity creates a very wide fifth vertebral, indicating a fusion of the fourth costals with V5. The larger Leiden specimen (RMNH 10187) originally collected by Dr. Ten Kate has this deformity with a symmetrical pattern of three costals on each side and a very wide fifth vertebral (Fig. 5). Lidth de Jeude (1895) interpreted this as a normal pattern. One of Yowono's specimens

TABLE 2. BASIC EXTERNAL DIMENSIONS OF *CHELODINA MCCORDI*, ALL MEASUREMENTS IN MM. CL = CARAPACE LENGTH (STRAIGHT-LINE IN MIDLINE); CW = CARAPACE WIDTH (GREATEST); CD = CARAPACE DEPTH (GREATEST IN MIDLINE); PL-M = PLASTRON LENGTH (IN MIDLINE); PL-T = PLASTRON LENGTH (TOTAL, INCLUDING ANAL SPURS); PW = PLASTRON WIDTH (AT AXILLARY NOTCH); HW = HEAD WIDTH (TYMPANIC); J = JUVENILE; F = FEMALE; M = MALE; U = UNKNOWN SEX.

Specimen Number	Sex	CL	CW	CD	PL-M	PL-T	PW	HW
RMNH 4349	j	99.5	73.0	31.0	76.0	81.0	43.5	18.6
AGJR 460	f	150.0	118.0	49.0	119.5	126.0	70.0	25.1
AGJR 455	m	150.5	114.5	49.5	117.5	124.5	67.0	26.3
AGJR 454	m	151.0	116.5	47.0	115.5	123.5	66.0	25.0
MCZ 176731	m	153.0	120.5	47.5	116.5	125.0	67.0	26.0
AGJR 449	m	155.0	123.5	51.5	121.5	128.0	73.0	25.3
AGJR 367	f	159.0	121.0	52.0	124.0	131.0	71.0	26.3
AGJR 456	m	162.5	127.5	53.5	120.5	130.5	70.0	25.0
AGJR 369	u	163.0	125.0	52.0	123.0	132.5	71.0	—
RMNH 10187	u	179.5	140.0	60.0	138.0	147.0	81.5	28.7
AGJR 457	f	180.0	137.0	60.0	138.0	147.0	80.0	28.7
AGJR 448	f	181.5	143.5	63.5	139.0	146.5	81.5	27.8
AGJR 366	f	182.0	142.5	60.0	145.0	153.0	84.5	27.9
MCZ 176732	f	194.0	152.0	67.0	153.0	162.0	85.0	30.5
MCZ 176730	f	197.5	156.0	67.5	150.5	159.5	86.5	29.6
AGJR 452	f	202.0	159.0	73.0	161.5	171.0	93.0	31.2
AGJR 365	f	206.0	162.0	72.0	161.0	171.0	92.0	31.8
AGJR 453	f	213.0	162.0	77.5	162.5	172.0	95.0	32.8

(AGJR 368) has this identical deformity, and another (AGJR 365) has it on one side only. Five specimens have markedly reduced fourth costals, often on one side only, giving a slightly wider asymmetrical fifth vertebral. One of the specimens with this deformity is the smaller Leiden specimen (RMNH 4349) originally collected by Dr. Ten Kate.

Width relationships of marginal scutes 1 and 2 distinctive, with M1 much narrower than M2 as measured along the V1-C1 scute border. M1 typically half as wide as M2. In *C. pritchardi* M1 is wider or subequal to M2, and in *C. novaeguineae* M1 averages about 80% of the width of M2 (Fig. 7).

Carapace slightly less broad in *C. mccordi* than in *C. pritchardi*, but significantly broader than in *C. novaeguineae*. Lateral marginal recurving typical for *C. mccordi*, not present in *C. pritchardi*,

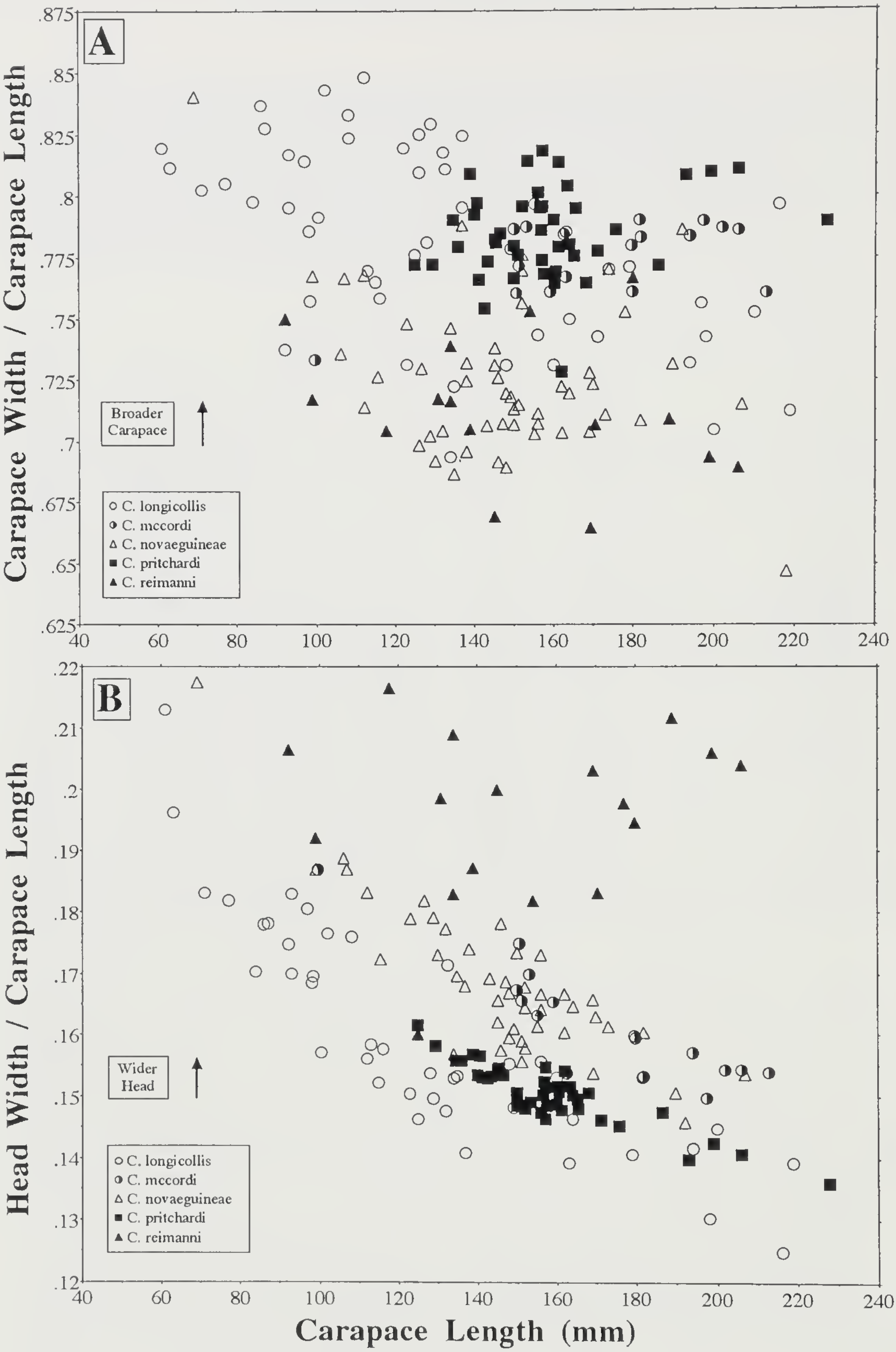


Figure 6. (Part 1). Shell morphometrics. Graphs plotting morphometric variation for four species of *Chelodina* subgeneric group "A", showing the relationships of: **A.** carapace width ratio (Carapace Width/Carapace Length); **B.** head width ratio (Head Width/CL).

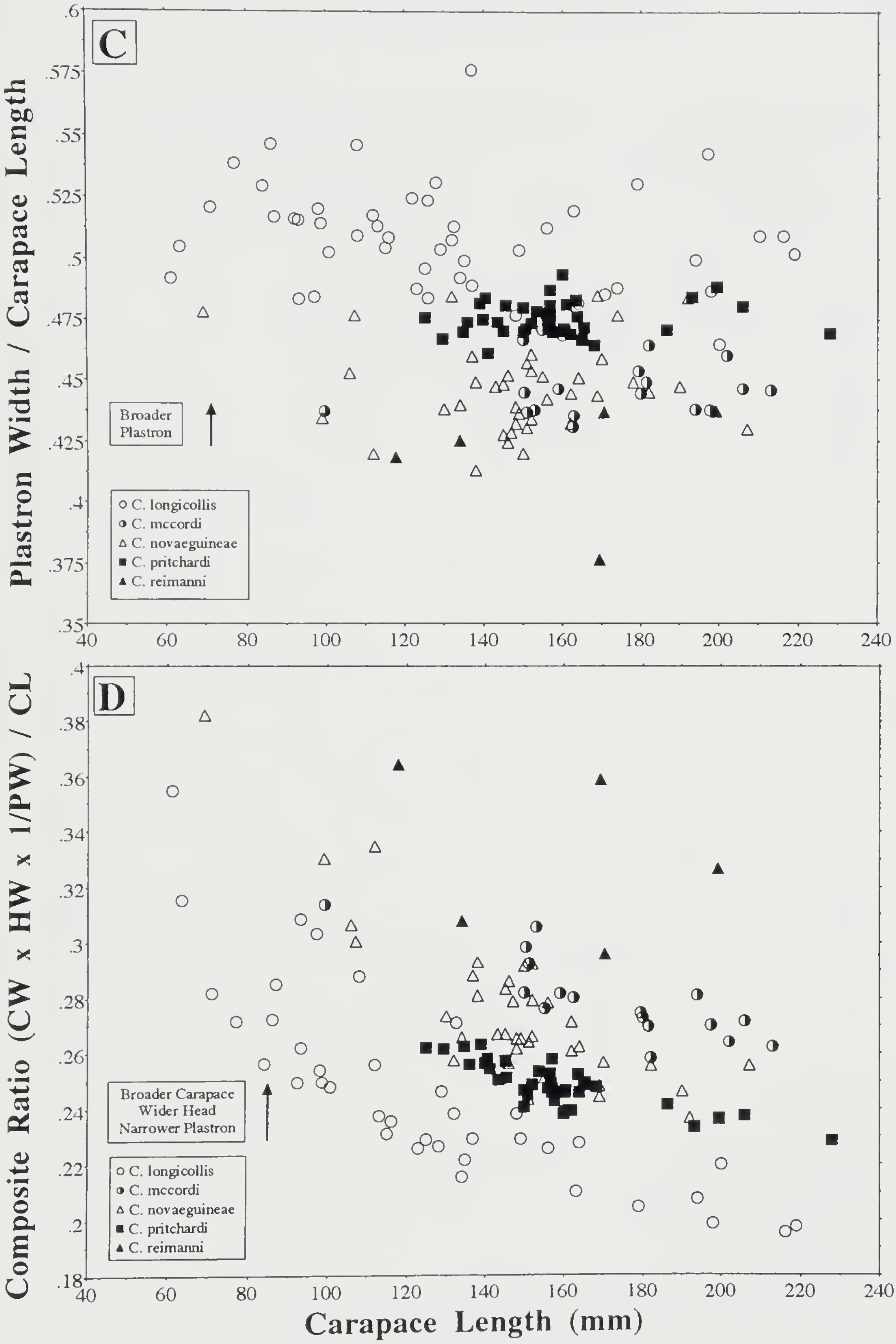


Figure 6. (Part 2). Shell morphometrics. **C.** plastron width ratio (Plastron Width/CL); and **D.** composite ratio of (CW × HW × 1/PW)/CL expressed as a trivariate product; all versus Carapace Length. Note the position of *C. mccordi* as most similar to *C. pritchardi* in terms of carapace width (A), but most similar to *C. novaeguineae* in terms of head width (B), plastron width (C), and composite ratio (D).

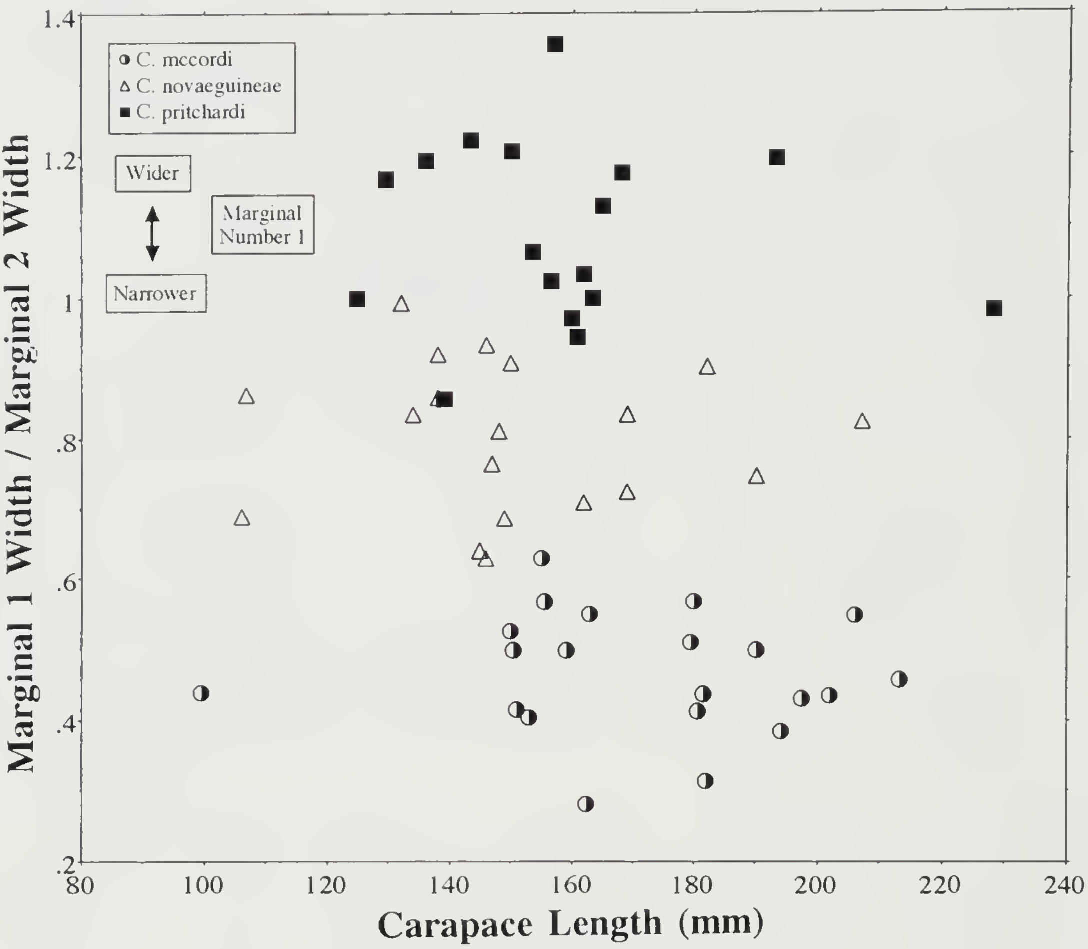


Figure 7. Shell morphometrics. Graph plotting morphometric variation for M1/M2 ratio (marginal number 1 width/marginal number 2 width) versus carapace length for *Chelodina mccordi, C. pritchardi,* and *C. novaeguineae,* showing that *C. mccordi* has M1 about half as wide as M2, *C. pritchardi* has M1 slightly wider or subequal to M2, and *C. novaeguineae* has M1 about 0.8 times as wide as M2.

not present or only very minimally developed in *C. novaeguineae.* Supracaudal ridging with adjacent mild marginal concavity also typical for *C. mccordi,* not present in *C. pritchardi* or *C. novaeguineae.*

Carapace moderately deep in large specimens, relatively flatter in younger ones. No sexual dimorphism in carapace depth of specimens examined, with like-sized males and females with same carapace depth. Older females of larger body size all with deeper shells. Carapace depth in *C. mccordi* slightly deeper than in either *C. pritchardi* or *C. novaeguineae.*

Color variable, with most specimens having a distinctive light grayish-brown carapace unusual for *Chelodina* subgeneric group "A". Some specimens darker chestnut brown, more typical of the color seen in *C. novaeguineae* and *C. pritchardi.* Carapace scutes moderately rugose with retention of concentric growth lines only in small specimens.

Plastron. Plastron broad, axillary width averaging 57.9% of midline plastral length. Anterior lobe moderately broad, similar to *C. novaeguineae,* but not as broad as *C. pritchardi* [Fig. 6(2)-C]. Slight expansion of anterior plastral lobe at posterior edge of humeral scutes, similar to *C. pritchardi.* Anal notch moderately deep, no sexual dimorphism noted. Intergular broad, long, and without marginal contact. Plastral scute medial length formula Ig > An ≥ Abd > Fem > Pec > Gul. *C. pritchardi* usually with Pec ≥ Fem, *C. novaeguineae* with either Pec > Fem or Fem > Pec. No axillary or inguinal scutes.

Plastron color light yellowish-white with many specimens having thin irregular light-brown areas along the plastral sutures. Original specimens of Dr. Ten Kate with oxidized plastrons, all of Yowono's specimens without oxidation. Plastron most similar to *C. pritchardi,* but generally with more pigment. Hatchlings with a beautiful orange and gray pattern covering plastron and ventral soft parts, gradually fading with growth (McCord, personal communication).

Head and Soft Parts. Head with small irregular scales covering temporal skin, smooth over parietal and interorbital roof. Neck with low soft tubercules, generally more similar to *C. pritchardi* than the slightly more prominent, firmer tubercules in *C. novaeguineae.* Soft parts light to moderate gray dorsally, whitish ventrally, generally lighter in color than in either *C. pritchardi* or *C. novaeguineae.* Hands and feet with four claws each.

Head width moderately wide, similar to the relatively broad-headed *C. novaeguineae,* significantly wider than the narrow-headed *C. pritchardi* and *C. longicollis* [Fig. 6(1)B], and narrower than the broad-headed *C. reimanni.* Head width not as wide as in the broad-headed members of *Chelodina* subgeneric group "B" (*C. expansa, C. rugosa, C. siebenrocki, C. parkeri,* and *C. oblonga*). Relative narrowing of the head ontogenetically.

A few specimens of "*C. novaeguineae*" said to come from Roti, but provided without reliable data, have broad heads most similar

TABLE 3. MEANS AND STANDARD DEVIATIONS FOR SHELL MEASUREMENT RATIOS OF THREE *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 2. DATA BASED ONLY ON SPECIMENS OF CARAPACE LENGTH GREATER THAN 100 MM. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NOT AUSTRALIAN ONES. M1 = WIDTH OF MARGINAL NUMBER 1, M2 = WIDTH OF MARGINAL NUMBER 2; FOR THIS MEASUREMENT ONLY, *C. PRITCHARDI* N = 17 AND *C. NOVAEGUINEAE* N = 19.

Ratio	*C. pritchardi* (n = 43)	*C. mccordi* (n = 17)	*C. novaeguineae* (n = 51)
CW/CL	.785 ± .018	.779 ± .012	.723 ± .028
PW/PL-M	.610 ± .012	.579 ± .010	.576 ± .018
HW/CL	.150 ± .005	.160 ± .007	.167 ± .010
CD/CL	.328 ± .014	.335 ± .015	.327 ± .021
M1/M2	1.089 ± .129	.465 ± .090	.803 ± .105

to *C. reimanni* and extremely deep robust shells of a dark black color. These distinct animals appear to represent a different taxon and have been excluded from this analysis of *C. mccordi,* awaiting further confirmation of their probably disparate geographic origin.

Size and Sexual Dimorphism. The largest specimen of *C. mccordi* recorded is a female of 213 mm carapace length. The largest male examined has a carapace length of 162.5 mm, indicating probable sexual dimorphism, with females larger than males. Calculating the sexual dimorphism index according to the method of Gibbons and Lovich (1990) yields an SDI value of approximately 1.31 for *C. mccordi.* The SDI for *C. pritchardi* is 1.22, that for New Guinean *C. novaeguineae* 1.37. The maximum size recorded for *C. pritchardi* is 228 mm, and for New Guinean *C. novaeguineae* 218 mm (Rhodin, 1993). However, in general, and for most specimens representing typical mature adults, *C. mccordi* is significantly larger than New Guinean *C. novaeguineae,* slightly smaller than *C. pritchardi,* and significantly smaller than Australian *C. novaeguineae,* which reaches carapace lengths of 279 to 300 mm (Cann, 1978; Rhodin, 1993).

Osteology

Skull. The description of skull osteology is based on the examination of 36 skulls of *Chelodina* subgeneric group "A". Of these, 4 are *C. mccordi,* 6 *C. pritchardi,* 7 *C. longicollis,* 15 *C. novaeguineae* (12 from New Guinea, 3 from Australia), 2 *C. stein-*

TABLE 4. BASIC SKULL MEASUREMENTS FOR *CHELODINA MCCORDI*. SL = SKULL LENGTH (SNOUT–OCCIPITAL CONDYLE); SWT = SKULL WIDTH, TYMPANIC MAXIMUM; SWM = SKULL WIDTH, MAXILLARY MAXIMUM; SDM = SKULL DEPTH AT POSTERIOR EDGE OF MAXILLAE; SD = SKULL DEPTH IN MIDLINE BETWEEN SUPRAOCCIPITAL SPINE AND BASISPHENOID; IOW = INTER-ORBITAL WIDTH, MINIMAL; OW = ORBITAL WIDTH, SHORT AXIS; PTW = PTERYGOID WIDTH, MINIMAL; TW = TRITURATING WIDTH, MAXILLARY (MEASURED IN MIDLINE FROM TOMIAL EDGE TO ANTERIOR CHOANAL BORDER). REFER TO TABLE 5 AND FIGURES 8(1) AND 8(2) FOR ANALYSIS OF SKULL MEASUREMENT RATIOS.

Specimen Number	SL	SWT	SWM	SDM	SD	IOW	OW	PtW	TW
AGJR 449	35.5	24.5	20.2	8.8	10.0	3.7	8.4	11.9	4.7
RMNH 10187	40.1	27.7	22.9	9.5	11.0	4.3	8.9	13.2	5.7
AGJR 452	43.6	30.1	25.6	10.1	12.1	4.9	9.5	14.2	6.6
AGJR 453	45.5	32.0	25.9	10.6	13.4	5.5	9.6	14.5	7.1

dachneri, and 2 *C. reimanni.* Refer to Tables 4 and 5 and Figure 8 (parts 1 and 2) for additional skull measurements and ratios, and Figure 3 for skull illustrations of *C. mccordi.* Comparative figures of skulls of *C. pritchardi, C. novaeguineae, C. reimanni,* and *C. longicollis* are in Rhodin (1993).

The skull of *C. mccordi* is a typical *Chelodina* subgeneric group "A" type skull, not overly elongate, flattened, or wide as in subgeneric group "B". It is strikingly similar to *C. pritchardi* and differs markedly from *C. novaeguineae.* Like in *C. pritchardi,* the skull of *C. mccordi* is differentiated from *C. novaeguineae* by its relative lack of robusticity. *C. novaeguineae* has wide and robust

TABLE 5. MEANS AND STANDARD DEVIATIONS FOR SKULL MEASUREMENT RATIOS OF THREE *CHELODINA* SPECIES. ABBREVIATIONS AS IN TABLE 4. *C. NOVAEGUINEAE* INCLUDES ONLY NEW GUINEAN SPECIMENS, NOT AUSTRALIAN ONES.

Ratio	*C. pritchardi* (n = 6)	*C. mccordi* (n = 4)	*C. novaeguineae* (n = 15)
SWT/SL	.648 ± .013	.694 ± .006	.687 ± .024
SWM/L	.553 ± .006	.574 ± .009	.532 ± .032
SD/SL	.290 ± .009	.282 ± .009	.320 ± .018
TW/SL	.144 ± .005	.145 ± .010	.194 ± .009
PtW/SWT	.522 ± .014	.472 ± .014	.461 ± .018
IOW/OW	.470 ± .037	.503 ± .056	.570 ± .055

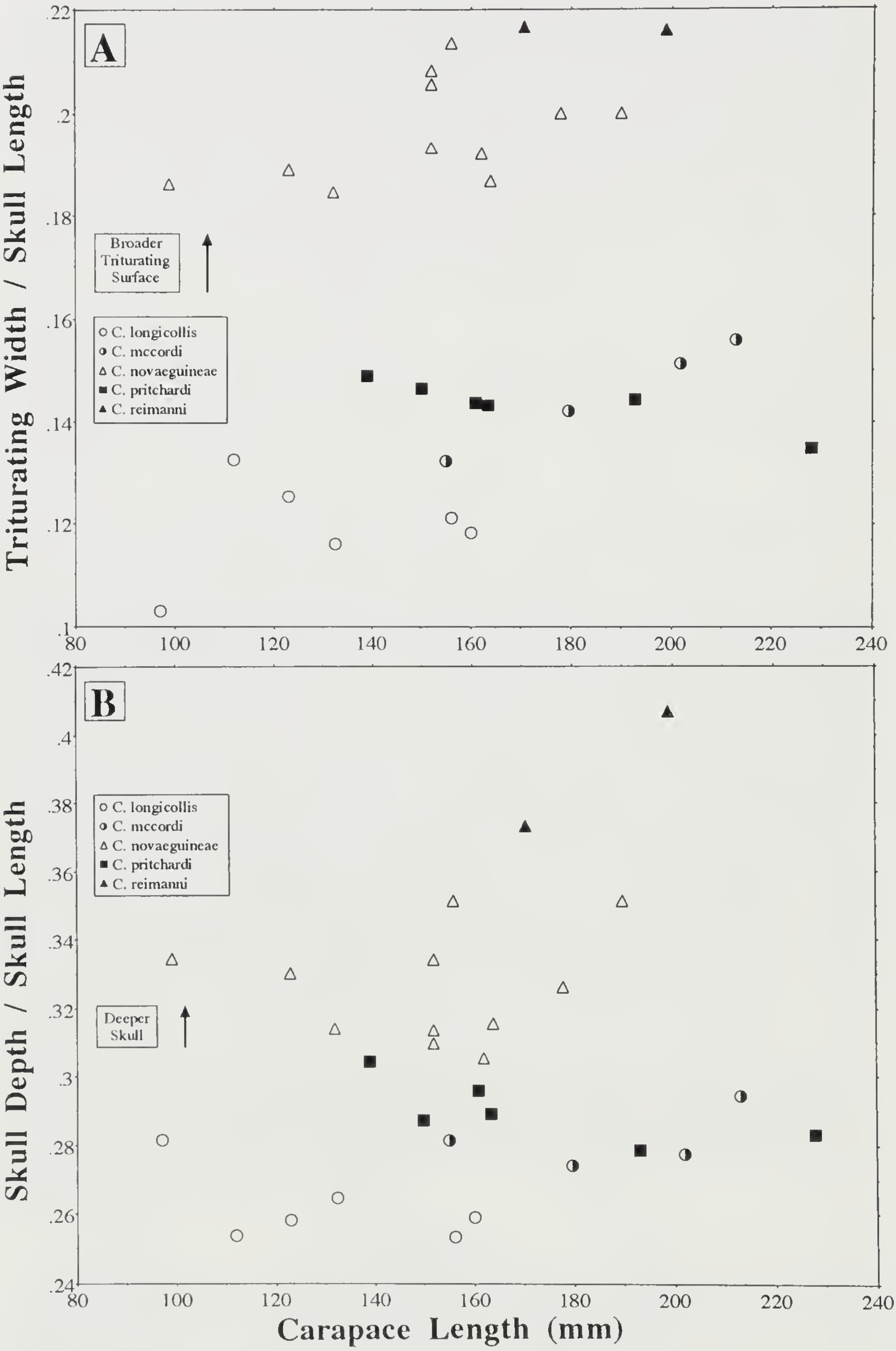


Figure 8. (Part 1). Skull morphometrics. Graphs plotting morphometric variation for four species of *Chelodina* subgeneric group "A", showing the relationships of: **A.** maxillary triturating width ratio (TW/Skull Length); **B.** skull depth ratio (SD/SL).

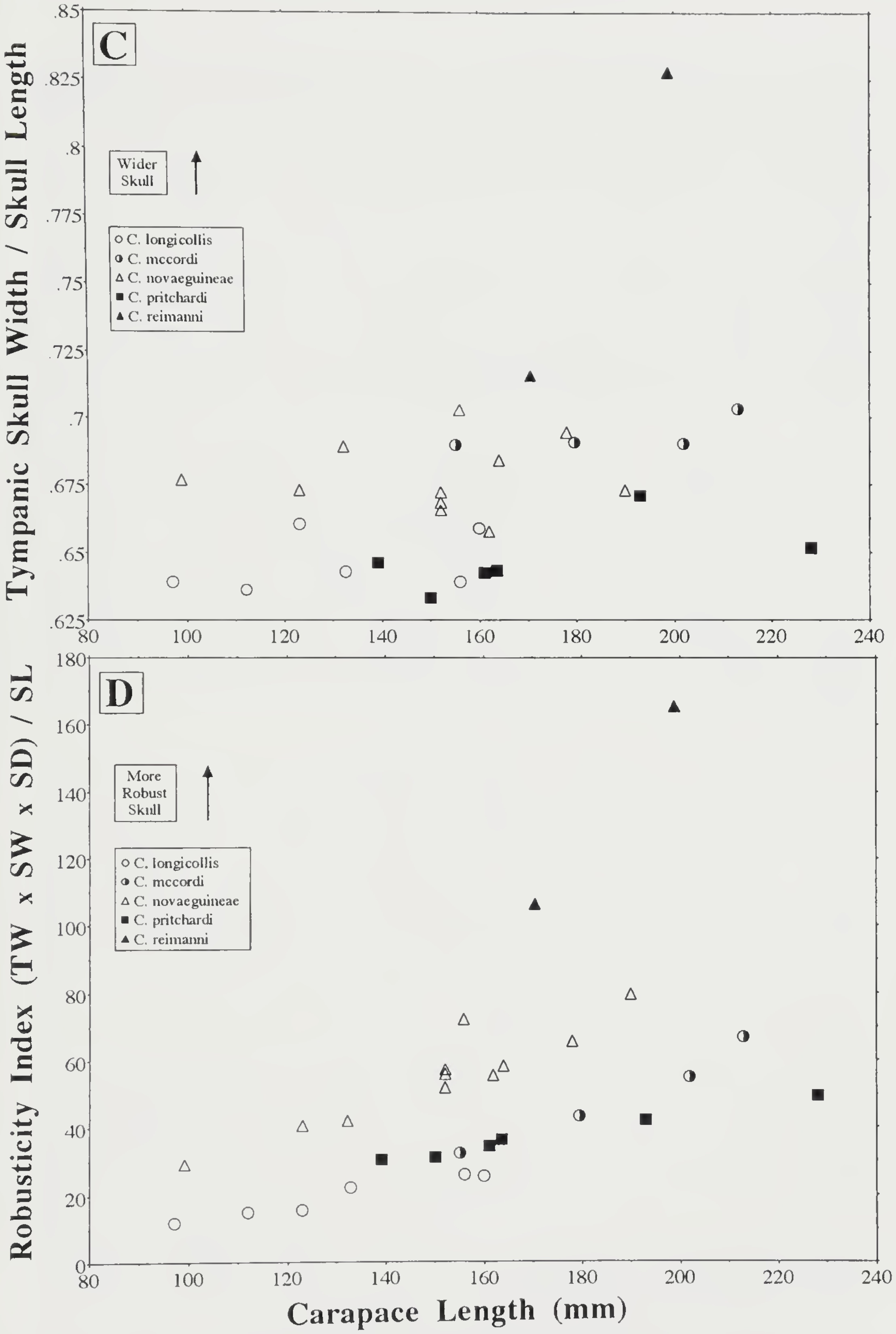


Figure 8. (Part 2). Skull morphometrics. **C.** tympanic skull width (SWT/SL); and **D.** composite graph of Robusticity Index (TW × SWT × SD)/SL expressed as a trivariate product; all versus Skull Length. Note the position of *C. mccordi* as most similar to *C. novaeguineae* in terms of tympanic skull width (C), but most similar to *C. pritchardi* in terms of triturating width (A), skull depth (B) and composite Robusticity Index (D).

maxillary and mandibular triturating surfaces, with correspondingly wide and robust horny rhamphothecae. *C. longicollis* has very thin triturating surfaces, whereas both *C. pritchardi* and *C. mccordi* have surfaces that are intermediate and similar to each other, though *C. mccordi* tends to have slightly wider surfaces in larger specimens [Fig. 8(1)A]. *Chelodina novaeguineae* has a deep skull, *C. longicollis* a shallow skull, and *C. mccordi* and *C. pritchardi* have skull depths that are intermediate and similar to each other [Fig. 8(1)B]. Skull width as compared to skull depth is greater in both *C. mccordi* and *C. novaeguineae,* while *C. longicollis* and *C. pritchardi* have relatively narrower skulls [Fig. 8(2)C]. *Chelodina mccordi* has an intermediate-sized parietal roof, like *C. pritchardi,* not as large as *C. longicollis* or as reduced as *C. novaeguineae.* The pterygoid trochlear processes are minimally divergent and unflared in *C. mccordi,* as they are in *C. pritchardi,* lacking the extreme flaring and prominent divergence seen in *C. novaeguineae.* The skull depth and supraoccipital crest height are similar in *C. pritchardi* and *C. mccordi.*

The Robusticity Index (see Rhodin, 1993) for the skull of *C. mccordi* is very similar to *C. pritchardi,* but shows a slight increase in skulls of larger specimens, related to slightly increased triturating width and skull depth, and moderately increased skull width in the larger specimens. Both of these species have skulls that are much more robust than *C. longicollis* and much less robust than *C. novaeguineae* [Fig. 8(2)D], with *C. mccordi* generally slightly more robust than *C. pritchardi.*

Overall, the skull of *C. mccordi* seems to represent a phylogenetic intermediate step in a transformation series leading from *C. pritchardi* to *C. novaeguineae. Chelodina mccordi* retains narrow triturating surfaces, though they are slightly widened, and a shallow skull; but has developed significantly increased skull width with slightly increased skull robusticity. These features correlate with an increase in temporal muscle mass, intermediate between the relatively reduced mass in *C. pritchardi* and the markedly increased mass in *C. novaeguineae.* Evidently *C. mccordi* has developed the need for moderately increased mandibular adductor force generation in its jaw closure mechanism, but has not reached the point of requiring massively enlarged opposing triturating crushing surfaces.

From skull morphology, one would predict that *C. mccordi* is a generalized carnivore or omnivorous scavenger, intermediate between the presumed specialized molluscivorous *C. novaeguineae* and the more limited piscivorous or carnivorous *C. pritchardi.*

Cervical Spine. Central cervical articulation pattern is (2(3(4(5)6)7(8) in 4 specimens (2 by direct exam, 2 by radiographic investigation), the only known pattern for all Chelidae as described by Williams (1950). Atlanto-axial (C1-C2) cervical morphology in *C. mccordi* identical to the pattern in other *Chelodina* subgeneric group "A".

Shell. No neural bones in 2 specimens, all pleurals meeting in the midline. Axillary buttress moderately robust, articulating with lateral first pleural and posterior third peripheral; inguinal buttress less robust, articulating with postero-lateral edge of fourth and antero-lateral edge of fifth pleurals, as well as anterior seventh peripheral. Suprapygal relatively wide, contacting tenth peripheral. Broad contact between first peripherals and first pleurals.

Ecology and General

Reproduction. Radiographs or dissections were performed on the females in the series, with one female demonstrating multiple small ovarian follicles bilaterally, as well as enormous paired cloacal bursae (one on each side). No eggs were noted. Reproductive parameters have not yet been fully documented for the species, but McCord (personal communication) has hatched several clutches of eggs from captive individuals. Average clutch size is 8–9 eggs, with oval eggs similar in shape to *C. longicollis* and *C. pritchardi,* but slightly larger than for either of those species, and slightly smaller than the eggs of *C. reimanni,* which are larger and more rounded. The eggs have hatched in about 2 months when incubated at about 82°F.

Growth. The smallest specimen of 99.5 mm carapace length shows three concentric growth rings. The rings are clearly visible on the costal scutes and allow for measurements of growth. The first ring encompasses the indistinguishable original scute and subsequent growth in the first season; the second ring, growth through the end of the second season; and the third ring, growth until capture. By measuring the corresponding costal-vertebral suture lengths for each of the rings it is possible to create a ratio of costal length to carapace length for each ring and thereby calculate the carapace length of the animal at the end of each growth season. By this method, this specimen (RMNH 4349), which is now 99.5 mm long at the end of its third and last growing season, was approximately 73.5 mm long at the end of the second season, and 51.0 mm long at the end of the first season. The actual original hatchling scute is no longer visible, but extrapolation from the regression curve created by the first three values yields an expected hatchling size of about 32.0 mm (Fig. 9). This predicted hatchling size is within the range of hatchlings of other species of *Chelodina* I have examined: *C. parkeri* at 35.0 mm, *C. siebenrocki* at 35.0 mm, *C. rugosa* at 32.0 mm, *C. oblonga* at 30.0 mm, and *C. longicollis* at 28.8 mm. It is of course not known whether the growth rings are reflective of an annual cycle, but Roti has well defined wet and dry seasons, and it appears likely that this specimen is therefore about three years old.

Predation. Five large females display evidence of possible previous crocodile encounters. Four animals have what appear to be typical healed tooth holes and bite striations on the carapace, one has the hind portions of the carapace missing with resultant deformed regenerated scar tissue. The saltwater crocodile *Crocodylus porosus* is the most likely predator, but freshwater crocodiles may also occur in the Roti area (Ross, 1986). Native collectors also indicate that many specimens receive carapacial damage from farmers' plow blades in the rice paddies where the species is known to occur (McCord, personal communication).

Sympatry. No other freshwater turtles are known to occur on Roti, but the semi-aquatic emydid turtle *Cuora amboinensis* may well occur on the island, having previously been recorded on Timor (Iverson, 1986). In addition, the trionychid aquatic softshell turtle *Amyda cartilaginea* may occur on either Roti or Timor. Iverson (1986) records the nearest confirmed locality as Lombok Island just east of Bali, but *Trionyx cartilagineus newtoni* Ferreira, 1897, was described as having been obtained on Timor, and may represent evidence for a population in this area.

DISCUSSION

The occurrence of a population of chelid turtles on Roti Island in Indonesia comes as a relative surprise because of the known

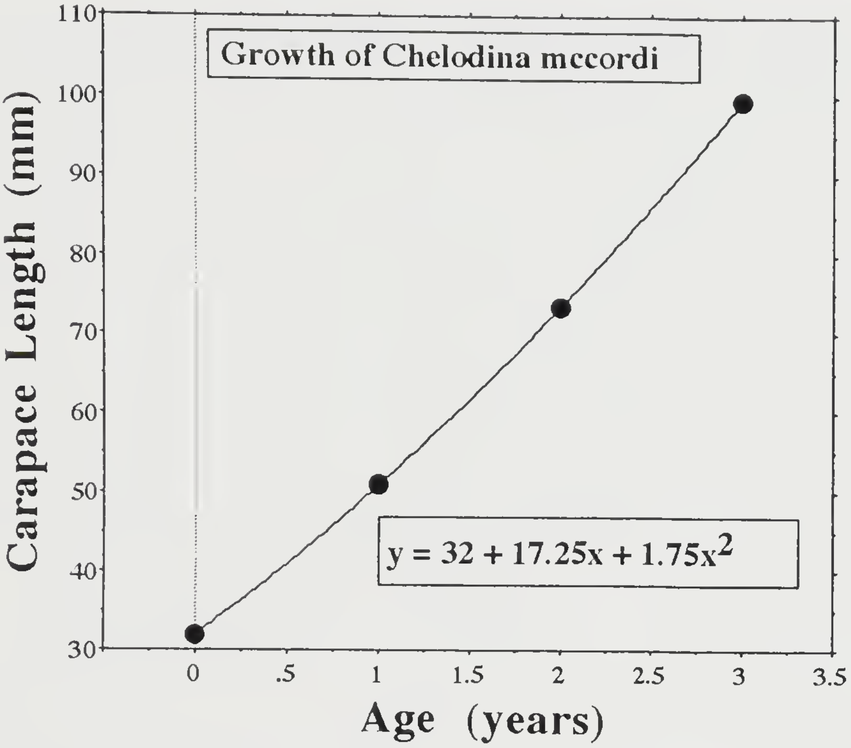


Figure 9. Graph showing probable growth of individual specimen of *C. mccordi* (RMNH 4349) as calculated by measurements of costal scute growth rings. Actual size of specimen recorded as last data point on graph; sizes at age 1 and 2 calculated from growth rings; size at age 0 extrapolated from the curve.

zoogeography of the family. Other than in South America, no other natural populations of chelid turtles have been recorded outside of continental Australia and New Guinea and islands on their contiguous Sahul Shelf. Although *Elseya novaeguineae* has been recorded in the Palau Islands in the northwestern Pacific (Aoki, 1977), that record probably represents an introduction. In addition, I have seen photographs of a specimen of *Emydura subglobosa* purportedly from New Britain in northeastern oceanic Papua New Guinea, which also probably represents an introduction. McCord (personal communication) has obtained specimens of this population of *Emydura subglobosa* collected in the vicinity of Rabaul, a major commercial center with a huge natural products market where exotic species introductions would come as no major surprise.

The collection of specimens of *C. mccordi* on Roti by Dr. Ten Kate back in 1891 and now by Frank Yowono about 100 years later confirms the presence of an established viable breeding population of this taxon. The demonstrated similarity in morphology of the original 1891 specimens and of the recently collected specimens confirms the identity and the source of the two series.

The marked morphological differences in *C. mccordi* from geographically proximate New Guinean and Australian *C. novaeguineae* argue strongly against recent introduction via human trade. In like manner, the significant similarities of *C. mccordi* with the more geographically distant southeastern New Guinean *C. pritchardi* argues against a recent introduction.

A more likely scenario to explain the presence of *C. mccordi* on Roti is the possibility that both *C. pritchardi* and *C. mccordi* represent relict populations of ancestral *Chelodina* subgeneric group "A" stock, living on the outlying periphery of the previously exposed margins of the continental Sahul Shelf during earlier periods of lower sea levels and shelf emergence (Jongsma, 1970; Doutch, 1972; Galloway and Loffler, 1972). During one of the periods that the Sahul Shelf was fully exposed to its 200 meter depth (Fig. 1), *C. mccordi* or its ancestor could potentially have reached Roti by rafting across the narrow deep oceanic channel that would have then separated the island from the northwestern shore of the exposed shelf. In addition, *C. pritchardi* could have reached southeastern Papua New Guinea across what would then have been a more broadly exposed Torres Strait land-bridge. Subsequently, with the partial submergence of the shelf the two species were left as peripheral, isolated, relict populations while the continental Australo-New Guinean form evolved into what is now *C. novaeguineae*. That large continental population then eventually became secondarily split by the much later appearance of Torres Strait separating New Guinea from Australia (occurring about 8,000 years ago), when sea levels rose to their present levels. This hypothesis is partially supported by the evidence found in skull morphologies, which suggests that both *C. mccordi* and *C. pritchardi* are intermediate between the primitive *C. longicollis* and the derived *C. novaeguineae*. In addition, it suggests a long period of isolation of both *C. mccordi* and *C. pritchardi* from "continental" *C. novaeguineae* stock. Further, it raises the possibility that New Guinean and Australian forms of *C. novaeguineae* may also be differentiating, as suggested by findings of slight differences in skull osteology between these two geographic isolates (Rhodin, 1993).

The time frame for this hypothesized phylogenetic scenario is hard to specify. The oldest known fossil of *Chelodina* is from the Early to Middle Miocene (ca. 28 million YBP) of northwestern Queensland, Australia (Gaffney *et al.,* 1989), and is very similar to modern representatives of the genus. It is certainly conceivable that much of the dispersal suggested above could have taken place during Late Miocene and Early Pliocene times (12–28 million YBP) when large land-bridge connections were present between New Guinea and Australia (Doutch, 1972; Galloway and Loffler, 1972). During this time there may even have existed some short-lived land-bridges between Australia and the southeastern Indonesian islands such as Timor and Roti (Doutch, 1972). Interestingly, one species of marsupial mammal from Australia (the cuscus, *Phalanger orientalis*) is found on Timor, also suggesting possible previous connections between the two areas (Cox, 1970), though Glover (1971) states that the cuscus probably represents an introduction by prehistoric man sometime later than 13,500 YBP (earliest evidence of man on Timor).

In addition, Jongsma (1970) has shown that the Sahul Shelf was fully exposed down to a depth of 200 meters as recently as the Illinoisan-Riss glaciation, about 170,000 years ago. Later, sea levels were again down to about 160 meters during the most recent Wisconsin-Wurm glaciation about 18,000 years ago. During these recent times, the Torres Strait land-bridge served as a continual connection between New Guinea and Australia between at least 80,000 and 8,000 years ago (Chappell, 1976).

It is therefore likely that *C. mccordi* reached Roti during one of several distinct times: 1) Late Miocene to Early Pliocene times, ca. 12–28 million YBP; 2) Illinoisan-Riss glaciation, ca. 170,000 YBP; 3) Wisconsin-Riss glaciation, ca. 18,000 YBP; or 4) introduced by prehistoric man sometime later than ca. 13,500 YBP. Other periods of potential dispersal probably also occurred between the Pliocene and Recent periods.

The phylogenetic relationships within *Chelodina* subgeneric group "A" have already been hypothesized and discussed by Rhodin (1993). Within the group, I regard *C. steindachneri* as the most primitive, with the group becoming more specialized and derived in a series that progresses through *C. longicollis, C. pritchardi,* and *C. novaeguineae* to *C. reimanni,* the most derived mem-

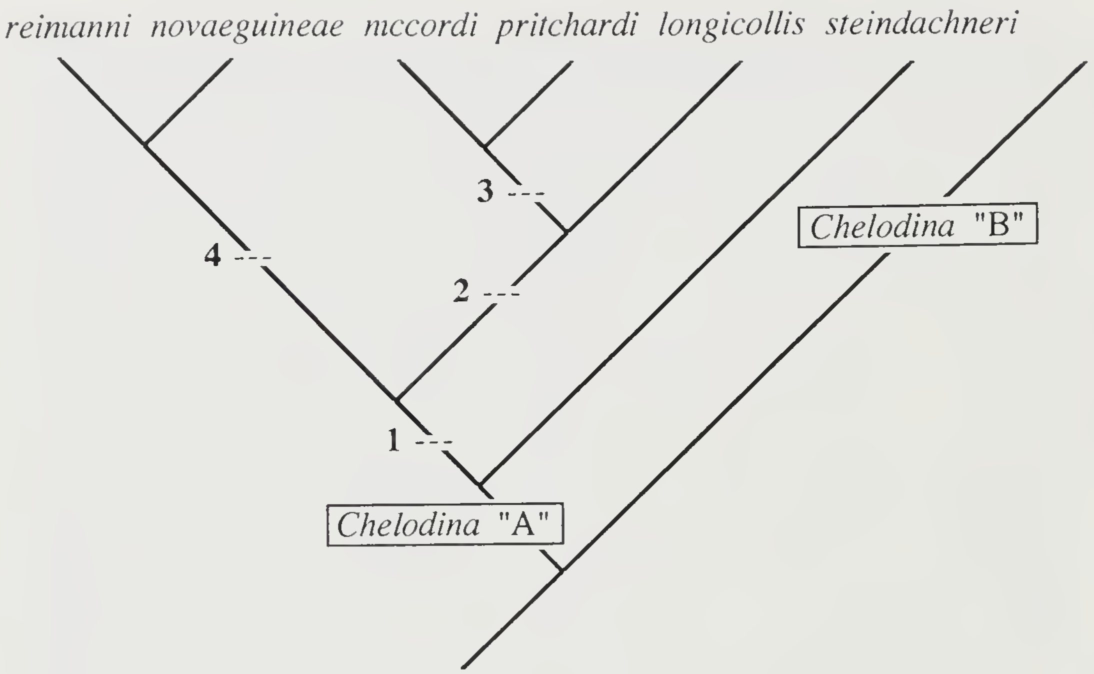


Figure 10. Hypothesized phylogenetic relationships of the six currently recognized species of *Chelodina* subgeneric group "A". The monophyly of *Chelodina* "A" follows Georges and Adams (1992). Characters supporting the intrageneric nodes are as follows: Node 1: partial or complete loss of chelid foramen; Node 2: wide parietal roof, narrow triturating surfaces, parallel pterygoids; Node 3: partial reduction in parietal roof width, slightly widened triturating surfaces; Node 4: narrow parietal crest, flaring pterygoids, wide triturating surfaces, deep robust skull.

ber of the group. Within this phylogeny, *C. mccordi* appears to be most closely related to *C. pritchardi* (Fig. 10), sharing the derived features of lack of chelid foramina and partially narrowed parietal roof, as well as the plesiomorphic features of a shallow skull, decreased robusticity, narrow triturating surfaces, and parallel pterygoid processes. The two species *C. reimanni* and *C. novaeguineae* share the derived features of a narrow parietal crest, flaring pterygoid processes, wide triturating surfaces, deep skulls, increased robusticity, and loss of chelid foramina.

In view of the isolated occurrence of *Chelodina mccordi* on the very small island of Roti, where available habitat may be limited, and human utilization pressures are perhaps heavy, an investigation into the population and survival status of the species needs to be undertaken. Basic ecological and life history data on the species are also extremely limited and further investigation is needed. Finally, the application of modern methods of molecular phylogenetic analysis to the species should be pursued to help confirm or falsify the hypothesized relationships presented here.

ACKNOWLEDGMENTS

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APPENDIX

Comparative material examined of *Chelodina longicollis, C. novaeguineae, C. pritchardi, C. reimanni,* and *C. steindachneri* all listed in Appendix in first paper of this series (Rhodin, 1993). See text for specimens of *C. mccordi* examined. Collection acronyms utilized in present paper are as follows:

AGJR = personal collection of Rhodin; MCZ = Museum of Comparative Zoology; RMNH = National Museum of Natural History, Leiden.

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AN ECOLOGICAL STUDY OF THE ENDEMIC HISPANIOLAN ANOLINE LIZARD, *CHAMAELINOROPS BARBOURI* (LACERTILIA: IGUANIDAE)

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AND JOSEPH PALUMBO, JR.

ABSTRACT. We studied the ecology and behavior of *Chamaelinorops barbouri* at two sites. *C. barbouri* has very specific habitat requirements: montane ravines with abundant leaf litter, well-shaded by intact forest canopy. It is an almost exclusively terrestrial lizard, preferring leaf litter in deep shade. Despite its non-basking, shade-loving habits, *C. barbouri* maintains its body temperature well above air temperature, and linear regression of body temperature and air temperature data yield a fairly low regression coefficient; this finding is surprising in comparison to the thermal biology of other forest-dwelling, non-basking anoles, and Greater Antillean anoles in general. We found *Chamaelinorops barbouri* to be cryptic, sedentary, and elusive, and thus difficult to study behaviorally. It is highly specialized ecologically, morphologically, and behaviorally for life in the leaf litter, much more so than any other anole.

INTRODUCTION

Since its discovery in 1919 by K. P. Schmidt, the anoline lizard *Chamaelinorops barbouri* has remained in animal of enigma. Over half a century passed from the time of Schmidt's (1919) description before the systematics and distribution of this endemic Hispaniolan anoline were worked out satisfactorily, and yet the precise type locality is still not known and probably never will be. This lizard has a unique vertebral column, not duplicated by any other vertebrate, of which the functional significance (if any) is still completely unknown (Forsgaard, 1983). Equally mystifying

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are the relationships of *Chamaelinorops*; it has been argued that the genus is either very derived (Etheridge, 1960; Wyles and Gorman, 1980), having arisen from within *Anolis,* or is very primitive (Williams, 1977; Case and Williams, 1987), indeed, the most primitive of living anoles.

Yet of all the enigmas of the biology of *Chamaelinorops barbouri,* we are most ignorant of its behavior and ecology. Our only information to date of *C. barbouri* behavior is limited to a single study of display behavior in captive males (Jenssen and Feely, 1991). No study has ever been conducted before on the ecology of *C. barbouri.* The sum of our knowledge in this area is limited to a few sentences on the preferred habitat (Thomas, 1966) and some remarks on the conditions under which eleven specimens were collected (Schwartz and Inchaustegui, 1980; Franz and Cordier, 1986). Our limitation in knowledge is primarily attributable to the inability of a non-native collector to procure a series of specimens. Only local residents of an area where *C. barbouri* is found are able to secure a series, usually with great ease. At the time of the most recent work on *Chamaelinorops* (Schwartz and Inchaustegui, 1980), a total of fifty specimens had been collected, of which the great majority (39) and the only large series (10) had been captured by natives.

Herein we report the results of an ecological study intended to elucidate some of the mysteries of the ecology and behavior of *Chamaelinorops barbouri.*

MATERIALS AND METHODS

A large series of *Chamaelinorops barbouri* can be obtained at a small settlement known to herpetologists as The Haitian Village and to natives as “Ande Javi,” located about 15 km SE of the town of Cabral and near the city of Barahona in the Provincia de Barahona, Dominican Republic. We received as many as 75 lizards collected by village residents in a “lizard market” in a two-hour period, and subsequently had to turn away additional specimens. Whereas no non-native had ever been able to collect more than a few *Chamaelinorops,* and then only serendipitously, and because it was unclear where to search for these lizards, we located a Haitian Village resident familiar with *Chamaelinorops* to act as a guide and to demonstrate how to collect them.

Study Site. There are two areas in the vicinity of The Haitian Village where *Chamaelinorops* is most abundant. Both are close to the village, located in ravines sloping to a dry stream bed. The slopes have been cleared of most of the understory and planted with food plants under an intact mesic primary forest canopy (and hence much shade), and are covered by abundant leaf litter often interspersed with small, crushed limestone rocks.

The first site (1,000 m elevation) is called Caña Segudinas by natives. A small portion of slope on one side of a ravine has been burned out and planted over with *malanga*‘, a tuberous crop with large leaves. Penetrating further into the forest, one encounters the dry stream bed and mostly uncultivated ravine slopes where *Chamaelinorops* is found.

The second site (1,140 m elevation) is known by the villagers as Tejul. This site includes broadleaf forest, and an adjacent coffee plantation where the canopy is still intact and most of the understory has been cleared and planted over with coffee trees. As with Caña Segudinas, the area is a ravine whose slopes descend to a dry stream bed.

Methods. To collect *Chamaelinorops,* residents of The Haitian Village require only a short stick (about 2–3 ft long). The collector must walk slowly, brushing the leaf litter with the stick in moderately short, slow strokes while paying close attention to any movement. When encountered, the lizard betrays its presence by a short hop or run, followed by an abrupt stop or a dive beneath the litter. If not clearly sighted and kept track of during flight, *Chamaelinorops* is easily lost by dint of its superb camouflage and its ability to rapidly hide within the leaf litter.

Our study was conducted from 28 July 1985 to 4 August 1985. We logged 15 person-days during the study period, collecting data on 70 *Chamaelinorops barbouri.* The optimal time for observing *Chamaelinorops* was throughout the morning and into the early hours of the afternoon, and so most of our study was conducted between 0900 and 1400 hrs.

The study focused on three aspects of the biology of *Chamaelinorops barbouri*: (1) habitat preference; (2) thermoregulatory strategy; and (3) behavior. For habitat preference the “Rand census” was employed. The observer walks through the habitat, recording the height, diameter, and insolation of the perch where the lizard was first sighted (Rand, 1964). Perch height was recorded as "underground," "ground," or estimated to the nearest foot. Because *Chamaelinorops* is almost completely terrestrial, one of five categories was recorded for every ground observation: on dead leaves, under dead leaves, on bare earth, on rocks, or under rocks. For perch diameter, seven categories were used: underground, on rocks, on ground covered with leaf litter, on bare ground, trunk (perch diameter greater than three inches), branch (perch diameter between one-half inch and three inches), and twig (perch diameter less than one-half inch). For insolation, the amount of shade at the perch was estimated as one of the following: full shade, moderate shade, light shade, or unshaded. For thermoregulatory data, Schultheis quick-reading mercury thermometers were inserted into the cloaca as soon as possible after lizard capture in order to minimize hand contact with the lizard's body. Once sighted, *Chamaelinorops* was easy to capture; all lizards were captured within five seconds, eliminating the possibility of false body temperature elevation due to a protracted chase. The air temperature 1 cm above the perch site was then immediately recorded with the thermometer bulb shaded, after the bulb was completely dry. Cloacal temperatures were recorded for 64 of the 70 *Chamaelinorops* sighted. For behavioral data, individuals were often observed for several minutes before or after capture. Additional observations were also made on captive individuals maintained in a terrarium.

Thermoregulation was assessed by the method of Huey and Slatkin (1976), using the regression coefficient from the linear regression of body temperature and air temperature: a regression coefficient near 0 implies careful thermoregulation (body temperature independent of air temperature), whereas a regression coefficient near 1 implies thermoconformity (complete thermal passivity). A Spearman's coefficient of rank correlation of body and air temperature data was also calculated. There was no significant difference (t-test of the differences between two means, $P \gg 0.05$) between the body temperatures of adult males and adult females, and, although there was a significant difference between the body temperatures of adults and juveniles ($0.05 > P > 0.02$), the sample size of juveniles (3) was too small to be

Table 1. Perch height observations for *Chamaelinorops barbouri*. Perch height categories: −G = underground; G = ground; all other categories are estimates to the nearest foot. (Unsexed adults = adults observed but not captured.)

	−G	G	0	1	2	3	4	5
Males		35	1					1
Females	1	25	1			1		
Juveniles		2	1					
Unsexed adults		2						
Totals	1	64	3			1		1

useful; consequently all sex and age classes were pooled in the presentation of thermoregulatory data. The standard criterion of statistical significance was utilized ($P < 0.05$). All statistical tests follow Sokal and Rohlf (1981).

RESULTS

Observations at the two study sites indicate that *Chamaelinorops* has the following special habitat requirements: (1) An intact forest canopy providing abundant shade; (2) Abundant leaf litter; (3) Conditions (1) and (2) located in a ravine with slopes ending in a dry stream bed (the association with a dry stream bed in both of our study sites may have been a coincidental finding, but we never succeeded in finding *Chamaelinorops* in habitats meeting conditions (1) and (2) but not (3), and *Chamaelinorops* collected for us by residents from the Sierra de Neiba on the North Island of Hispaniola were always reported as having come from habitats exhibiting the above three conditions); (4) Montane elevations, usually about 1,000 m (but can range from 300 m to 1,710 m [Schwartz and Inchaustegui, 1980]).

Data on perch height (Table 1) indicate that *Chamaelinorops* is almost exclusively a terrestrial anole and not at all arboreal. *Chamaelinorops* was never observed in any type of situation that could be considered arboreal—trees, saplings, bushes, low vegetation, etc.—despite intensive searches for lizards in these situations. Although it is possible that *Chamaelinorops* was missed in arboreal situations due to its extremely cryptic appearance and

Table 2. Types of terrestrial perches chosen by *Chamaelinorops barbouri.*[1]

	On rocks	Under rocks	On dead leaves	Under dead leaves	Bare earth
Males	1	1	24	5	5
Females	1	2	15	3	4
Juveniles			1	1	
Unsexed adults		1		1	
Totals	2	4	40	10	9

[1] Other terrestrial situations in which a single individual was observed: on a log, underground, on a dead banana leaf, within a pile of dead branches on dead leaves.

habits, lizards could never be induced to climb, even when placed next to or on arboreal perches and provoked to a state of severe alarm or agitation.

Chamaelinorops predominantly prefers ground covered with leaf litter (Tables 2 and 3). *Chamaelinorops* was observed on dead leaves more frequently than on all other terrestrial perches combined (Table 2). Similarly, the number of observations of *Chamaelinorops* on leaf litter exceeded the number of observations on all other categories of perch diameter combined (Table 3). In addition, no observations for the trunk or twig categories were recorded.

Chamaelinorops overwhelmingly prefers shady perches to sun-

Table 3. Perch diameter observations for *Chamaelinorops barbouri.* Tr = trunk (>3″ in diameter); Br = branch (½″–3″ in diameter); Tw = twig (<½″ in diameter). (See Materials and Methods Section in text for additional explanation of perch diameter categories.)

	Underground	Rock	Ground covered by leaf litter	Ground	Tr	Br	Tw
Males		1	30	6			
Females	1	1	20	6			
Juveniles			2			1	
Unsexed adults			1	1			
Totals	1	2	53	13		1	

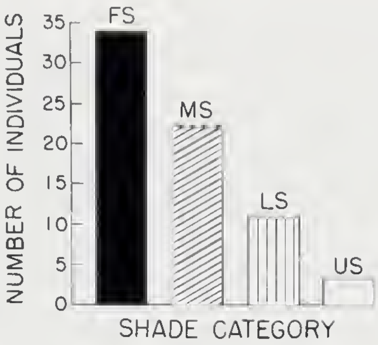

Figure 1. Shade category observations for *Chamaelinorops barbouri.* FS = full shade; MS = moderate shade; LS = light shade; US = unshaded.

ny ones. About half of our observations found *Chamaelinorops* in full shade, and lizards were seen in full and moderate shade (the two categories with the greatest shade) in over three-quarters of all observations (Fig. 1). Indeed, only three of 70 individuals were observed in unshaded conditions, over 11 times less frequently than in full shade.

Seven lizard species are sympatric with *Chamaelinorops* at the study sites, including five species of anoles (Fig. 2). None of the other lizard species substantially overlaps with *Chamaelinorops* in its habitat preference.

The endemic Hispaniolan anguid *Wetmorena haitiana mylica* can be found in the same forest situation as *Chamaelinorops,* but is encountered only under rocks and appears to be a burrower. It occurs not only in well-shaded forest habitats but also in disturbed, open habitat, as long as there are rocks for it to hide under. The second anguid lizard at the study sites, *Celestus costatus oreistes,* is seen only in open, disturbed habitat and never is syntopic with *Chamaelinorops.*

Five species of *Anolis* are found at the study sites, and all occur primarily in ecotone habitat where the forest abruptly meets the heavily disturbed, open areas. Five of Williams's (1983) ecomorphs are represented. There are two trunk-crown ecomorph species, *Anolis coelestinus* (a trunk-crown I ecomorph species = large) and *A. singularis* (a trunk-crown II ecomorph species = small). Both occur on leaves and branches of the canopy and upper trunk of trees. *Anolis distichus* is a trunk ecomorph species, occurring primarily on tree trunks between the trunk-crown and trunk-ground species. *Anolis cybotes* is a trunk-ground species,

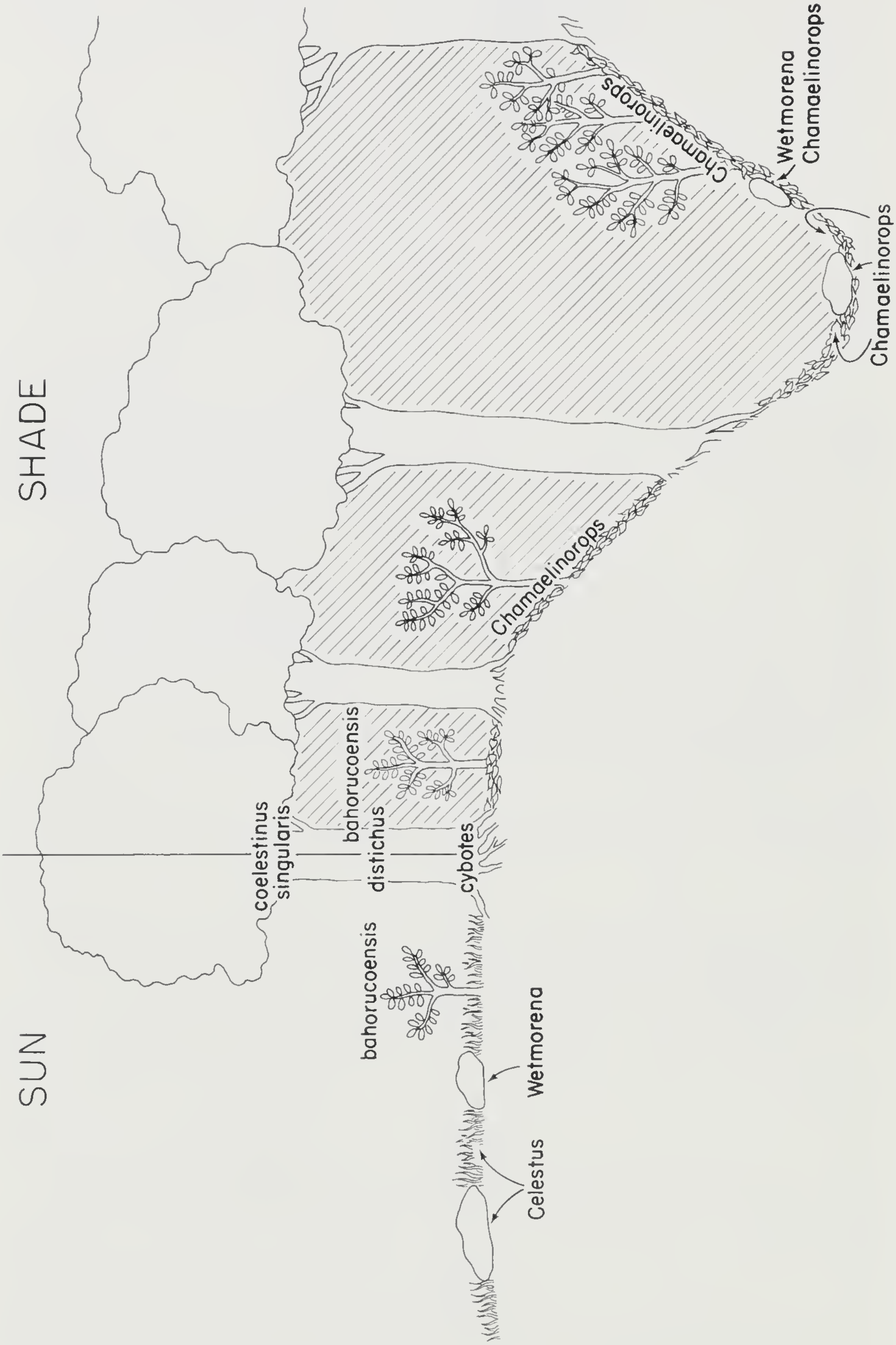
SUN
SHADE
coelestinus
singularis
bahorucoensis
distichus
cybotes
bahorucoensis
Wetmorena
Celestus
Chamaelinorops
Chamaelinorops
Wetmorena
Chamaelinorops
Chamaelinorops
Chamaelinorops

TABLE 4. THERMAL BIOLOGY DATA FOR *CHAMAELINOROPS BARBOURI*.[1] T_B = BODY TEMPERATURE; T_A = AIR TEMPERATURE; N = NUMBER OF INDIVIDUALS OBSERVED; $\bar{x} \pm SD$ = MEAN PLUS OR MINUS ONE STANDARD DEVIATION; R_S = SPEARMAN'S COEFFICIENT OF RANK CORRELATION OF BODY AND AIR TEMPERATURES.

		T_B		T_A	
	N	$\bar{x} \pm SD$	Range	$\bar{x} \pm SD$	Range
Males	36	25.6 ± 1.4	22.0–31.0	22.3 ± 1.5	20.0–26.0
Females	23	26.4 ± 2.0	22.0–30.0	22.8 ± 1.5	21.0–27.0
Juveniles	3	27.5 ± 0.5	27.0–28.0	23.8 ± 2.0	22.0–26.0
Unsexed adults	2	28.2 ± 1.8	27.0–29.5	24.0 ± 1.4	23.0–25.0
Total	64	26.0 ± 1.9	22.0–31.0	22.6 ± 1.5	20.0–27.0

[1] $r_S = 0.521$ ($P < 0.001$).

occurring on the lower trunks of trees and on the ground, usually in close proximity to a tree trunk. *Anolis bahorucoensis* is found primarily on bushes (bush ecomorph). Of the five *Anolis, A. coelestinus* and *A. singularis* are rarely encountered at the study sites, and only *A. bahorucoensis* and *A. distichus* are common in or near forests inhabited by *Chamaelinorops.* Of all *Anolis, A. bahorucoensis* penetrates the forest most deeply (although still primarily an ecotone species) and on several occasions was collected on bushes in *Chamaelinorops* habitat.

Given that *Chamaelinorops* shows such a strong preference for well-shaded habitat, we were surprised to discover that its mean body temperature (MBT) is well above the mean air temperature (MAT) (Table 4 and Fig. 3). The MBT is 26.0°C, and ranges from 22.0°C to 31.0°C; the MAT is 22.6°C and ranges from 20.0°C to 27.0°C. The difference between the MBT and the MAT, $\bar{x}_{TB} - \bar{x}_{TA}$, is about 3.5°C. Linear regression of body temperature and air temperature yields a regression coefficient of 0.69, suggesting *Chamaelinorops* is more of a thermoconformer than a thermoregulator.

The very patchy abundance of *Chamaelinorops,* both spatially

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Figure 2. Perch and climatic preferences for the eight lizard species occurring at The Haitian Village study sites. Names beginning in lower case letters are species of *Anolis.* Hatched lines represent shaded habitat.

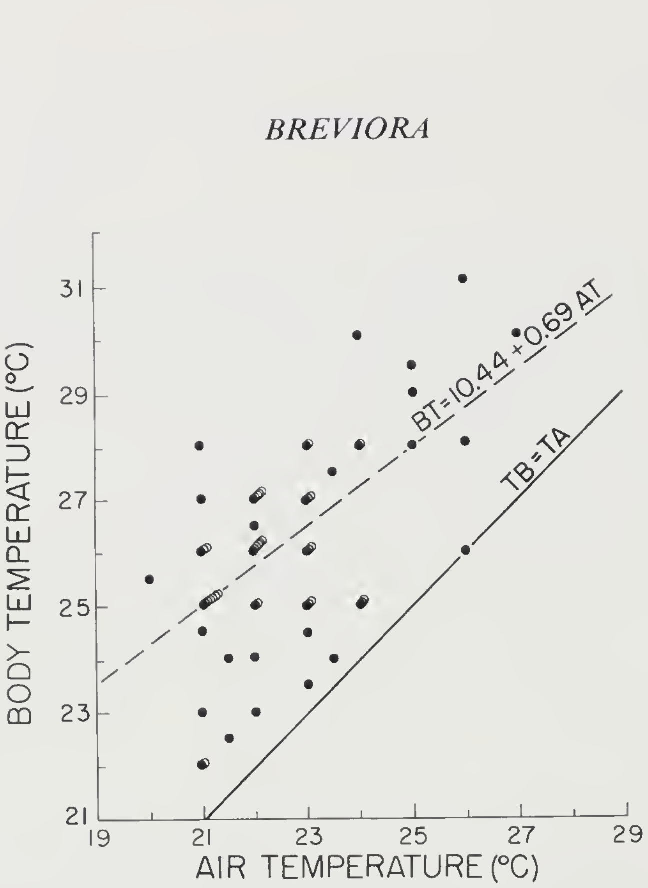

Figure 3. A plot of the body temperature and air temperature data for *Chamaelinorops barbouri.* The solid line represents the isothermal line (body temperature = air temperature, $T_B = T_A$). The dashed line is the linear regression of body temperature and air temperature, for which the equation is provided. The correlation coefficient (r_S) = 0.52. Multiple individuals with the same data are depicted by overlapping circles.

and temporally, was impressive. *Chamaelinorops* only occurs in the selected areas around The Haitian Village where its stringent habitat requirements are met; elsewhere in the area it appears to not occur at all. It is abundant only during the morning hours and early afternoon; after 1400 hrs, *Chamaelinorops* completely disappears. Additionally, even when we visited ideal habitat at ideal hours where the previous day *Chamaelinorops* had been found in abundance, on some occasions, it was difficult or impossible to find any lizards.

Data on behavior is limited, primarily due to the sedentary habits and cryptic nature of *Chamaelinorops.* We often attempted to observe individuals in the field, but were continually rewarded with nothing but a prolonged view of an immobile lizard (even after up to 15 minutes of observation). Observations on captive individuals yielded similar results. We became most familiar with *Chamaelinorops* escape behavior, which usually consists of a very brief scampering dash or series of hops (of no more than several inches) followed by an abrupt freeze. This tactic proves quite effective: the leaf litter, bare earth, and crushed limestone background beautifully conceal a stationary *Chamaelinorops* with its color pattern of black markings on pale white, gray, and tan tones, and an outline that closely resembles a dead leaf. When pressed further, *Chamaelinorops* often dives into the leaf litter. If it does not dive into the leaf litter, *Chamaelinorops* continues its initial tactic of a brief dash or series of hops followed by an abrupt stop, starting and stopping until the threat abates or an object to hide behind is encountered. When subjected to a prolonged threat, *Chamaelinorops* seems to tire quickly, increasingly abbreviating the flight and extending the stationary portion of the escape.

When captured, males can be quite aggressive, holding out the stark black dewlap, opening the mouth to expose the black mucosa, and even producing a weak bite if greatly agitated. Females and juveniles were never observed exhibiting such behavior when captured, and indeed one could reliably identify a male by such aggressive behavior alone. *Chamaelinorops* also moved abruptly and became quite agitated when one of us produced high-pitched whistles and bird-like clicking sounds (resembling the call of grackles).

Although no behavioral interactions were observed in the field, on several occasions multiple individuals were found together in a small area, including one observation of five individuals in a three by three meter area. One question which still remains unsettled is whether *Chamaelinorops* burrows. One individual was found under several inches of sandy soil and stones, and several were collected under rocks and leaf litter (Table 2). Residents of The Haitian Village believe *Chamaelinorops* burrows, and we were shown holes in which lizards were believed to live. However, we never found lizards after excavating such holes, and in captivity individuals were never observed to burrow despite being provided with ample soil in terraria.

DISCUSSION

General Ecology. Chamaelinorops barbouri is the only known West Indian anole specialized for life in leaf litter. Indeed, of all the anoles, only *Anolis humilis* from Central America approaches *Chamaelinorops* in its preference for leaf-litter habitat (Brattstrom

TABLE 5. *CHAMAELINOROPS BARBOURI* AND *ANOLIS HUMILIS* COMPARED. DATA FOR *A. HUMILIS* IS FROM FITCH (1973, 1975).

Feature	*Chamaelinorops barbouri*	*Anolis humilis*
Snout–vent length	Usually <50 mm	<45 mm
Color	Light brown/tan with variable pattern	Dark brown/olive with variable pattern
Dewlap	Small, black with yellow edge	Large, red with yellow edge
Modal perch	On ground, mostly leaf litter, marked shade preference	Often leaf litter, but mostly above ground on buttressed roots of large trees; marked shade preference
Body proportions	Head relatively short, body compressed, long limbs, very long tail	Stout body, short limbs and tail
Scales	Middorsal scales greatly enlarged, keeled, 4–10 rows	Middorsal scales greatly enlarged, keeled, 8–12 rows
Foraging behavior	Sit-and-wait predator (?) on ground	Active forager on ground and buttressed roots of large trees
Defensive behavior	Primarily crypsis, via immobility, start and stop flight; always flees on ground, never climbs	Primarily crypsis, via start and stop flight; always flees towards tree root buttresses on ground or climbs tree base

and Howell, 1954; Fitch, 1973, 1975; Talbot, 1977). *Anolis humilis* exhibits several similarities to *Chamaelinorops* (Table 5), including small size, elements of the color pattern, yellow edging of the dewlap, preference for leaf litter and shade, greatly enlarged keeled middorsal scales, aspects of escape behavior, and absence of basking behavior (Fitch, 1973, 1975). However, the two anoles differ markedly in a number of other features which directly reflect the greater specialization of *Chamaelinorops* for life in leaf litter. *Chamaelinorops* is exclusively terrestrial and predominantly found in leaf litter, whereas *A. humilis* spends much of its time above ground and, when in leaf litter, is almost always centered around buttress roots of large trees. *Chamaelinorops* relies more on staying immobile or hiding, and flees only on the ground; *A. humilis* is much more mobile and usually flees toward trees, occasionally "squirreling" around the tree base to the opposite side of the threat. In form, *Chamaelinorops* more closely resembles a dead leaf, with the "body extremely compressed, the sides vertical or concave . . ." (Schmidt, 1919) and an overall angular appearance, compared to the "stubby-bodied" (Fitch, 1975) *A. humilis.* So, in every way—ecologically, behaviorally, and morphologically—*Chamaelinorops* is more specialized for life in leaf litter than *A. humilis.* Indeed, *Chamaelinorops* is the only known true leaf-litter specialist among all of the anoles for which ecological information is available.

Although no other West Indian anole is a leaf-litter specialist, three species are known to be as markedly terrestrial as *Chamaelinorops. Anolis armouri* and *A. shrevei* of the Dominican Republic are commonly found under stones, and *A. armouri* also perches horizontally on fallen logs (E. E. Williams, in lit.). Ruibal (1964) provided a description of the habitat preferences of the Cuban *A. ophiolepis,* which is of interest in comparison to *Chamaelinorops*: "This is not a rare species; it is merely rarely caught. This is the only truly terrestrial species of the Cuban anoline lizards. The species is found in pastures and savannas, on the ground and runs to take refuge in grass tussocks. I have observed the species sleeping on the leaves of small bushes."

We tentatively suggest that the shared terrestrial habitat preferences and behaviors seen in *Chamaelinorops* and these three *Anolis* may represent a "weak" ecomorph, a "ground" category. Certain anole ecologies, such as a preference for ground habitat, may not select for strong, completely congruent behavior and/or morphology. This may reflect the great variability of ground habitats (in soil types, cover such as leaf litter versus grass, open surfaces versus dense undergrowth, to name a few) as compared to a more uniform surface such as a tree trunk. Thus, these four "ground" anoles, although alike in their terrestriality and particular behaviors, are morphologically different, in contrast to the "standard sequence" ecomorphs (Williams, 1983) which show strong correlations among morhpology, ecology, and behavior.

Data on perch height preference in *Chamaelinorops* show that it is an exclusively terrestrial anole. In situations where it was not clear whether an individual might have chosen a perch above ground level, we always decided in favor of the greatest perch height category possible. However, in all five such observations, stone or boulder perches were involved which closely resembled the ground in having leaf litter and/or moss cover; furthermore, these perches never arose abruptly but were in continuous and gradual contact with the ground. Hence, to *Chamaelinorops,* such perches are probably just another varied portion of the constantly changing ground surface. If *Chamaelinorops* ever climbs above the ground, it appears to be a rare exception.

The observations of others (Schwartz and Inchaustegui, 1980; Franz and Cordier, 1986) are largely in agreement with our data, except some cases of use of low arboreal perches have been noted. Schwartz and Inchaustegui (1980) reported that all but two specimens for which they had information came from ground situations; one individual was found ". . . at night sleeping totally exposed on the curving bare branch of a small woody legume 0.3 m above the ground surface," and another was ". . . in a crevice in a large tree about 1.2 m above the ground in a field being actively cut and weeded by a number of native workmen." Franz and Cordier (1986) found all but three and their specimens in ground situations; three specimens were collected ". . . among twigs in dead shrubs," but no perch height was provided.

Our data suggest that observations of diurnal arboreality in *Chamaelinorops* probably represent extreme circumstances or unusual instances. Our experiences suggest that the individual found 1.2 m above the ground in a large tree (Schwartz and Inchaustegui, 1980) may have been driven there by severe, immediate habitat destruction and disturbance, a situation and response unlikely to be observed under more natural conditions. The three individuals found among twigs in dead shrubs (Franz and Cordier, 1986) may actually have been on the ground within the matted twigs, a situation we frequently encountered. However, a sleeping individual found on a low arboreal perch (Schwartz and Inchaustegui, 1980) may represent either the true perch choice for sleeping *Chamaelinorops,* as is the case with most anoles, or unusual circumstance; we failed to observe *Chamaelinorops* sleeping, and, to date, this single observation is the only published report available.

The habitat preferences of *Chamaelinorops* appear to be rigidly specific. We believe that the specific habitat requirements we observed will be closely adhered to wherever *Chamaelinorops* is encountered, perhaps varying in the presence of a small stream, or the absence of a dry stream bed (but under mesic conditions). Although our study sites were in montane broadleaf forest canopy, it is not surprising that *Chamaelinorops* has also been found in montane pine forest (Franz and Cordier, 1986), the other type of Hispaniolan forest at higher elevations. In Haitian pine forest, Franz and Cordier (1986) found *Chamaelinorops* in ground situations, particularly in association with dead pine needles—the "leaf litter" of pine forests—and among their locality data ravines and basins are mentioned. Schwartz and Inchaustegui (1980) also noted *Chamaelinorops* in association with ravine habitat.

The patchy abundance of *Chamaelinorops,* both spatially and temporally, is striking. Its activities are apparently limited by the time of day and microhabitat requirements, and vary from one day to the next. Given the elusive habits and cryptic nature of *Chamaelinorops,* it is no wonder that, for decades, only experienced residents could collect it in any abundance.

Behavior. Although the sedentary nature, cryptic coloration, and elusive habits of *Chamaelinorops* prevented all but the most cursory portrait if this anole's behavior, some generalizations became apparent. Defensive behavior is based primarily on the use of camouflage and hiding: *Chamaelinorops* relies on immobility or short, abrupt starts and stops, along with leaf litter and other objects for hiding. Although foraging behavior was not observed, we suspect, as Schwartz and Inchaustegui (1980) have suggested, that *Chamaelinorops* is probably a "sit-and-wait" predator rather than an active pursuer, since its camouflage and sedentary tendencies well suit it for such a predation mode.

Whether *Chamaelinorops* burrows, as is claimed by residents of The Haitian Village, is still unclear. Supporting such claims is the observation of an individual under several inches of soil, and the testimony of several local residents. Contradicting these claims was our failure to unearth *Chamaelinorops* from alleged burrows pointed out to us by residents, and a lack of evidence of burrowing activity in any of the many individuals observed in captivity.

The possibility of burrowing lends an attractive potential functional explanation for the peculiar, extremely ossified vertebral column of *Chamaelinorops,* particularly in light of the resemblance of its vertebral column to that of only one other vertebrate, the mole *Scutisorex* (see Allen, 1917). However, as discussed above, the data available on burrowing is far from conclusive and the issue clearly deserves further investigation. Böhme (1982) hypothesized that the bony dorsal "shield" found in *Chamaelinorops* and certain chameleons of the genus *Brookesia* serves to deter bird predation by maintaining immobility and rigidity after being struck by a bird's beak. However, we observed conspicuous agitation and alarm elicited in *Chamaelinorops* in response to bird-like whistles and clicks, suggesting *Chamaelinorops* most likely responds to threatened bird predation in a more active than passive fashion. Besides a number of bird species, other potential predators encountered at the study sites are the colubrid snake *Antillophis parvifrons* and very large centipedes common under rocks.

It is clear from our discussion of *Chamaelinorops* behavior that it is quite difficult to obtain useful behavioral data on this cryptic, inactive, and highly elusive anole; ethological studies are patently needed but will demand the utmost in patient, careful observation and perseverance.

Themoregulation. Chamaelinorops was never encountered basking during this study. The possibility might be raised that we failed to observe basking because the exceptional camouflage of these lizards caused us to overlook some individuals, or startle tactics necessary for locating *Chamaelinorops* resulted in individuals moving out of sun patches too quickly for us to note basking. However, although we actively searched for *Chamaelinorops* in sun patches throughout the study, basking behavior was not observed (the three individuals observed in unshaded circumstances did not exhibit "classic" lizard basking behavior, i.e., they had not oriented and positioned their body to receive maximum solar radiation). Moreover, in the apparent preferred habitat of *Chamaelinorops,* sun patches are rare, small, and usually far apart even at midday, due to the thick forest canopy and frequent additional coffee trees, saplings or low bushes. Hence, we feel confident in stating that basking, if it occurs at all in *Chamaelinorops,* constitutes an insignificant proportion of this lizard's daily activities.

Given that *Chamaelinorops* was never observed basking and that it overwhelmingly prefers shaded deep forest habitat, the data on thermal biology is baffling (Table 4, Fig. 3). Huey and Slatkin (1976), in proposing a model of lizard thermoregulation, provided important predictions relevant to *Chamaelinorops* thermal biology: (1) Thermoregulation is beneficial only when associated costs are low. (2) The cost of raising body temperature should be proportional to the distance necessary for shuttling between sun and shade or hot and cold microenvironments. Thus, the cost of raising body temperature should be greater in closed forests than in more open habitats. (3) Lizards living in shaded forests (excluding the canopy), where costs of raising body temperature should be much higher than in open habitats (patches of sun for basking are more widely spaced in forests), tend not to bask and seemingly are relatively passive to ambient conditions. *Chamaelinorops* occurs exclusively in closed forests where patches of sun are few and far between; furthermore, *Chamaelinorops* shows a predominant preference for shade within such forest habitat (Fig. 1). Hence, the distance necessary for shuttling between sun and shade in *Chamaelinorops* habitat is great, and so is the cost of thermoregulation, by prediction (2) above. Since the thermoregulation is beneficial only when associated costs are low, *Chamaelinorops,* like many other lizards in shaded forests (Huey and Slatkin, 1976), should tend not to bask and should be relatively passive to ambient conditions. As one might predict, no basking behavior was observed, and *Chamaelinorops* was expected to be quite a thermoconformer, maintaining a body temperature varying little from ambient temperature.

However, as the data graphically and surprisingly depict (Table 4, Fig. 3), *Chamaelinorops* clearly maintains a body temperature well above air temperature, with the value of $\bar{x}_{TB} - \bar{x}_{TA}$ approximating 3.5°C. These data are even more impressive when compared with similar thermal data on other anoles (Table 6). Noteworthy is that the value of $\bar{x}_{TB} - \bar{x}_{TA}$ of *Chamaelinorops* greatly exceeds that of all the mainland shade-loving forest anoles for which data are available, and also well exceeds that of *Anolis allogus, A. gundlachi,* and *A. lucius,* the only purely shade-loving Greater Antillean forest anoles for which such data are available. Indeed, the $\bar{x}_{TB} - \bar{x}_{TA}$ of *Chamaelinorops* exceeds that of all but

Table 6. Comparison of the thermal biology of *Chamaelinorops barbouri* with all Greater Antillean and mainland shade-dwelling forest anoles for which appropriate data are available. $X_{TB} - X_{TA}$ = difference between mean body temperature and mean air temperature; regression coefficient = slope of the linear regression of body temperature and air temperature; NA = not available. With the exception of *C. barbouri*, all species listed are *Anolis*.

Species	$\bar{X}_{TB} - \bar{X}_{TA}$	Regression coefficient	Habitat	Reference
West Indian species				
Chamaelinorops	3.4	0.69	Deep-forest shade	This study
allisoni	0.8–1.6	NA	Open sunny areas	Ruibal, 1961
allogus	−0.8–−0.9	NA	Deep-forest shade	Ruibal, 1961
cooki	1.8	NA	Open, xeric areas	Huey and Webster, 1976
cristatellus	1.2	0.71	Open areas	Heatwole *et al.*, 1969
cybotes	1.4–3.1	0.41–0.76	Open areas	Hertz and Huey, 1981
distichus	NA	0.63	Mostly closed, shaded forest	Lee, 1980
gundlachi	0.4–0.5	1.08–1.13	Deep-forest shade	Hertz, 1981
homolechis	0.1–1.1	NA	Edge situations	Ruibal, 1961
longitibialis	1.1	0.83	Shaded portions of xeric areas	Hertz and Huey, 1981
lucius	−0.5–−0.9	NA	Deep forest shade	Ruibal, 1961
olssoni	2.3–3.1	0.7–0.89	Arid grassland and shrub	Hertz, 1974
sagrei	0.8-1.5	0.61–0.96	Open and closed areas	Lee, 1980; Ruibal, 1961
semilineatus	2.2–2.5	0.74–0.85	Mesic grassland and riparian	Hertz, 1974
shrevei	7.1	0.35	High montane grassland	Hertz and Huey, 1981
stratulus	0.9	0.77	Open park	Heatwole *et al.*, 1969

TABLE 6. Continued.

Species	$\bar{X}_{TB} - \bar{X}_{TA}$	Regression coefficient	Habitat	Reference
Mainland forest species				
gemmosus	0.6	NA	Cloud forest	Fitch *et al.*, 1976
humilis	1.0	NA	Deep-forest shade	Fitch, 1973
nigrolineatus	−0.6	NA	Cacao trees	Fitch *et al.*, 1976
polylepis	1.8	0.93	Deep-forest shade	Hertz, 1974
scypheus	1.1	NA	Rain forest	Fitch, 1968
taylori	1.2	NA	Dense woods	Fitch *et al.*, 1976

one Greater Antillean *Anolis, A. shrevei,* which is known to bask frequently (Hertz and Huey, 1981), in contradistinction to our observations on *Chamaelinorops.* Similarly, the regression coefficient of the linear regression of body temperature and air temperature for *Chamaelinorops,* 0.69, puts it distant to non-basking, shade-loving anoles like the Costa Rican *A. polylepis* (regression coefficient = 0.93; Hertz, 1974) or the Puerto Rican *A. gundlachi* (regression coefficient = 1.08–1.13; Hertz, 1981), but close to average for an open habitat, basking Greater Antillean anole, such as *A. cristatellus* or *A. cybotes* (Table 6). Hence, given that a regression coefficient of 0 represents perfect thermoregulation and 1 perfect thermoconformity (Huey and Slatkin, 1976), *Chamaelinorops* appears to be thermoregulating much more than it "should" be.

Chamaelinorops appears to be a shade-loving, non-basking anoline lizard that inhabits deep montane forest where sun patches are rare and costly to get to. How can it, then, maintain such a high value for $\bar{x}_{TB} - \bar{x}_{TA}$ and such a low regression coefficient for the linear regression of body temperature and air temperature? As an explanation for this enigma, three possibilities surfaced: (1) *Chamaelinorops* hides and/or sleeps beneath substrates that are warmer than air temperature. Bustard (1967) reported that geckos active at night can and may thermoregulate under bark or rock flakes during the day and achieve body temperatures near preferred levels. In order to utilize such a strategy, *Chamaelinorops* would have to use the limestone stones abundant in its habitat, in order to thermoregulate during the day. However, such stones are likely to heat up only in open habitat, not in the closed shady forest *Chamaelinorops* inhabits. (2) *Chamaelinorops* utilizes leaf litter, while both active and sleeping, to raise its body temperature. Leaf litter is a natural thermal insulator, and its decomposition generates some heat. *Chamaelinorops* could utilize the warmth retained or generated by leaf litter to raise its body temperature without necessarily having to bask. Though plausible, this explanation seems unlikely, given that leaf litter probably cannot generate adequate heat for a lizard. (3) *Chamaelinorops* may actually bask but was missed engaging in such activity during our study. This is always a distinct possibility, especially given that some deep-forest lizards, such as *Kentropyx calcaratus* (Rand and Humphrey, 1968), follow sun flecks on the forest floor. However, given that our insolation data do not indicate even the weakest correlation between *Chamaelinorops* perch selection and sun patches (Fig. 1) and that we never observed individuals sunning, we believe that this explanation may also be unlikely.

In summing up the paradoxical thermal biology of *Chamaelinorops* we can state only that resolution is not currently possible and must await more detailed study.

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THE PENNSYLVANIAN TEMNOSPONDYL *COCHLEOSAURUS FLORENSIS* RIEPPEL, FROM THE LYCOPSID STUMP FAUNA AT FLORENCE, NOVA SCOTIA

STEPHEN J. GODFREY[1] AND ROBERT HOLMES[2,3]

ABSTRACT. A previously undescribed skull of the Pennsylvanian cochleosaurid *Cochleosaurus florensis* Rieppel, from Florence, Nova Scotia, Canada, contributes the following characters to the generic diagnosis: extreme elongation of both the vomers and choanae, exclusion of the ectopterygoids and maxillae from the subtemporal fossae by a broad lateral ala of the pterygoid, and triangular tabular "horns." The transverse width of the skull through the midorbital region is less than the antorbital length. The configuration of the vomers and the general proportions of the palate resemble those of the Permian cochleosaurid *Chenoprosopus milleri* Mehl. The two genera are united in a monophyletic family—the Cochleosauridae—by the following autapomorphies: absence of the parietal foramen and lateral line sulci, subdued sculpturing on depressed areas of the dermal skull roof, an elongate antorbital region of the skull that is reflected in the palate by the greatly elongate vomers, ectopterygoid and maxilla excluded from the rim of the subtemporal fossa by a lateral ala of the pterygoid that makes contact with the jugal, and very long, triangular choanae.

INTRODUCTION

Members of the order Temnospondyli comprise the most numerous and diverse of all amphibian groups, enjoying a stratigraphic range extending from the Lower Carboniferous to the Lower Cretaceous. The superfamily Edopoidea has traditionally been identified as the stem group for the order (Carroll, 1988). Recent phylogenetic analyses (Milner, 1990a; Trueb and Cloutier, 1991) tend to confirm a relatively plesiomorphic status for those genera normally assigned to the group, but because their anatomy is incompletely known, this phylogenetic position, and even the integrity of the superfamily, is supported by few characters. Consequently, it is possible that the Edopoidea as presently constituted represents a structural grade within primitive tetrapods, and not a monophyletic group (Trueb and Cloutier, 1991).

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In 1956, four bone-bearing lycopsid stumps of the genus *Sigillaria* were excavated from the wall of an abandoned strip coal mine about 2 km north of Florence, Cape Breton County, Nova Scotia, Canada, by a field party from the Museum of Comparative Zoology, Harvard (MCZ). These stumps, all from a single horizon, were rooted about 4 m above the Lloyd Cove (Lower Bonar) Coal Seam of the Morien Group (Late Pennsylvanian), which probably corresponds in age to the Westphalian D of Europe (Carroll *et al.,* 1972). Reptilian remains from the stumps include the early protorothyridid *Palaeothyris acadiana* (Carroll, 1969) and the ophiacodontid synapsids *Archaeothyris florensis* and *Echinerpeton intermedium* (Reisz, 1972). Non-amniote tetrapods are represented by the limnoscelid *Limnostygis relictus* (Carroll, 1967a), the embolomerous anthracosaur *Carbonoherpeton carrolli* (Klembara, 1985), and the primitive temnospondyl *Cochleosaurus florensis* (Rieppel, 1980).

On the basis of two crushed but reasonably complete skulls of *Cochleosaurus florensis* (MCZ 4343 and 4344), Rieppel (1980) noted several similarities to *Chenoprosopus milleri* from the Lower Permian of New Mexico (Langston, 1953) and endorsed its assignment to the Edopoidea. Imperfect preservation, however, precluded detailed comparison of many anatomical features. Isolated postcranial remains subsequently attributed to *C. florensis* (Klembara, 1985) did little to clarify its taxonomic position. A third, more complete skull (MCZ 4342) from the same locality permits a more precise diagnosis of *C. florensis*, expands our knowledge of the family Cochleosauridae, and will contribute to a better understanding of the interrelationships of primitive temnospondyls.

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SYSTEMATIC PALEONTOLOGY

Order Temnospondyli Zittel, 1887

Superfamily Edopoidea Romer, 1945

Family Cochleosauridae Broili (in Zittel), 1923

Diagnosis. Temnospondyl amphibians with a maximum known snout–postparietal length of about 290 mm (*Chenoprosopus*). Parietal foramen and lateral line sulci absent. Extremely large premaxillae and vomers resulting in elongate antorbital region of the skull that exceeds skull width in midorbital region. Both external nares and elongate, anteriorly broadened choanae positioned well posterior to the tip of the snout. Ectopterygoid and maxilla excluded from the subtemporal fossa by a lateral ala of the pterygoid that forms a pterygoid–jugal contact.

Cochleosaurus Fritsch, 1885

Diagnosis. Temnospondyl amphibian with a maximum known skull length of 124 mm (snout–postparietal lappets). Sculpturing muted on depression on anterior part of lacrimal and on a median, depressed strip on the skull roof extending from the posterior margin of the postparietal to a shallow expanded depression on the snout. Lacrimal bears an anteroventrally directed ridge on its posterior half. Sculptured postparietal lappets. The choanae form a right-angled triangle with an anteriorly positioned base.

Cochleosaurus florensis Rieppel, 1980

Horizon and Locality. Morien Group, Westphalian D, Dominion Coal Co., strip mine no. 7 (abandoned), about 2 km north of Florence, Cape Breton County, Nova Scotia, Canada.

Diagnosis. Pterygoid with a broad ala that forms an extensive contact with the jugal to exclude the wedge-shaped posterior margin of the ectopterygoid and maxilla from the margin of the subtemporal fenestra. Shorter postparietal lappets and relatively wider skull table than *C. bohemicus.* Triangular tabular "horns" variably developed. At comparable skull lengths, dermal sculpturing in *C. florensis* comprises predominantly rounded pits rather

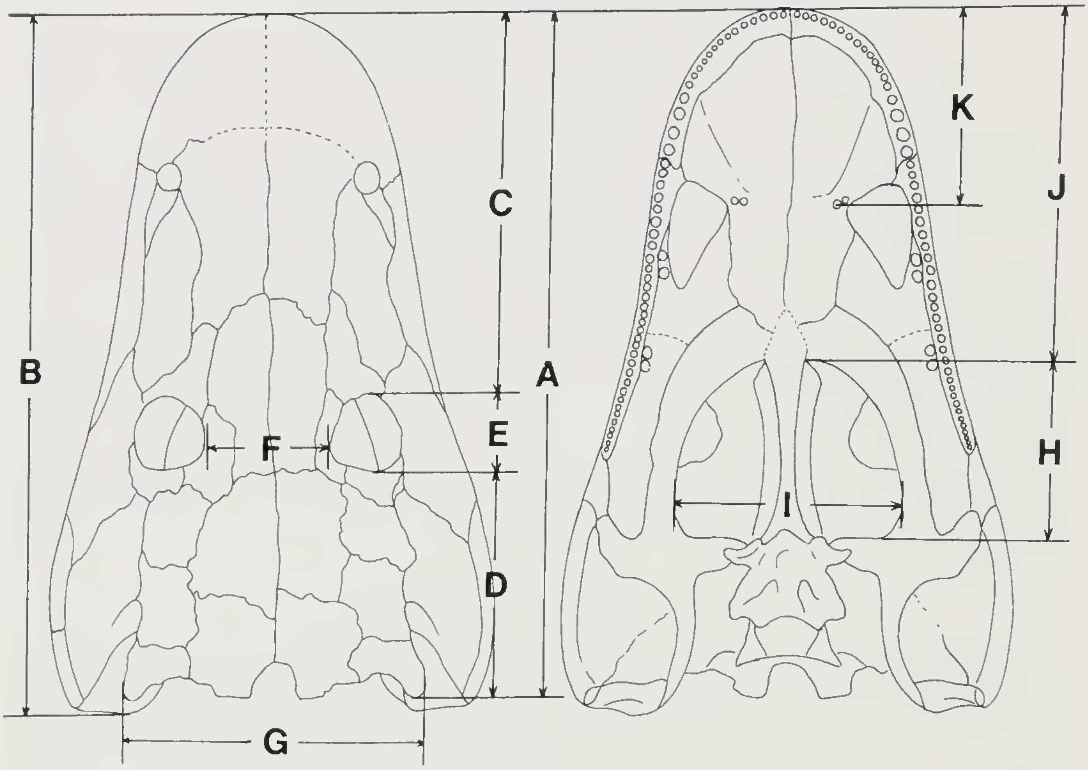


Table 1. Cranial dimensions of the skulls of *Cochleosaurus florensis* (in millimeters).

	MCZ 4342	MCZ 4343	MCZ 4344
A. Skull length (snout–tabular)	109	124	87*
B. Snout–quadrate length	108	123*	84*
C. Antorbital length	58	62	49
D. Skull table length	37	44	28
E. Orbital length	14*	18	12
F. Interorbital width	21*	27*	—†
G. Skull table width	47*	49*	30
H. Interpterygoid vacuity length	27	—	—
I. Interpterygoid vacuity width	29*	31	—
J. Snout–interpterygoid vacuity length	50	—	—
K. Snout–vomerine fang distance	29	26*	—

* Measurement estimated.

† — = Dimension not preserved or exposed.

than elongate grooves like those of *C. bohemicus,* indicating a smaller maximum (adult) size.

SPECIMENS EXAMINED

The following, comprising all known material attributed to *C. florensis,* were examined.

MCZ 4342: The most complete and least distorted skull of *C. florensis.* Both dorsal and ventral surfaces are almost completely free of matrix. This skull is slightly smaller than that of the holotype (Table 1).

MCZ 4343 (holotype): A severely crushed but articulated, largely complete skull; associated girdle and limb elements include a clavicle, a femur, and a tibia (Rieppel, 1980, text-fig. 1).

MCZ 4344: A small, dorsoventrally compressed skull originally prepared to expose the palate (Rieppel, 1980, text-fig. 3), but since then embedded in Carbowax (polyethylene glycol) and prepared to expose the dorsal aspect.

MCZ 2773: Isolated postcranial remains (Klembara, 1985, text-figs. 8, 9).

ABBREVIATIONS

a. cor—anterior coronoid
ang—angular
art—articular
c. pr—cultriform process
d—dentary
ect—ectopterygoid
f—frontal
it—intertemporal
j—jugal
l—lacrimal
m—maxilla
m. cor—middle coronoid
Mech—Mechelian fenestra
n—nasal
p—parietal
pa—prearticular
pal—palatine
para—parasphenoid
pm—premaxilla
po—postorbital
po. cor—posterior coronoid
pof—postfrontal
posp—postsplenial
pp—postparietal
prf—prefrontal
ps—parasymphyseal tusk
pt—pterygoid
q—quadrate
qj—quadratojugal
sa—surangular
sm—septomaxilla
sp—splenial
sq—squamosal
st—supratemporal
t—tabular
v—vomer

DESCRIPTION

Skull Roof

The skull of *Cochleosaurus florensis* (Fig. 1) resembles both *Cochleosaurus bohemicus* (Steen, 1938) and *Chenoprosopus milleri* (Langston, 1953) in having crocodiloid proportions with a broad, spatulate snout and flared cheeks, although the snout is somewhat broader than that of *Chenoprosopus.* Other proportional similarities include an antorbital region that exceeds its transverse width at the level of the orbits (the reverse of the condition seen in other Paleozoic temnospondyls such as *Caerorhachis* Holmes and Carroll, 1977; *Dendrerpeton* Carroll, 1967b, and Godfrey *et al.,* 1987; *Greererpeton* Smithson, 1982; *Neldasaurus* Chase, 1965; and *Edops* Romer and Witter, 1942, although shared by the eryopoid *Archegosaurus* Milner, 1978) and small dorsolaterally facing external nares located well back from the anterior margin of the snout. The orbits are variable in size (Table 1). The suspensorium projects only slightly posterior to the back edge of the skull table, resulting in a relatively anterior placement of the quadrate and shallower squamosal embayment as compared to the much larger *Chenoprosopus.* Similar intra- and interspecific, size-dependent variations, however, have been observed in other labyrinthodonts (Romer, 1939), rendering the taxonomic significance of such proportional differences to the Cochleosauridae ambiguous.

The parietal foramen and lateral line sulci are absent. Dermal ornamentation, as in other temnospondyls, consists primarily of course, rounded pits. However, unlike the type (MCZ 4343), some elongate grooves indicative of zones of rapid growth in immature individuals (Bystrow, 1935) are evident on some bones of both MCZ 4342 and 4344, especially the jugal and quadratojugal, although these are not as well developed as in *C. bohemicus.* The skull roof bears two conspicuous, broadly rounded, and coarsely sculptured longitudinal ridges, each passing anteriorly from the tabular along the margin of the skull table to the posterior rim of the orbit. Each wraps around the dorsal and anterior orbital borders, crossing the pre- and postfrontals as well as the lateral margin of the frontal, and then continues anteriorly along the lateral margin of the nasal, finally subsiding on the dorsolateral surface

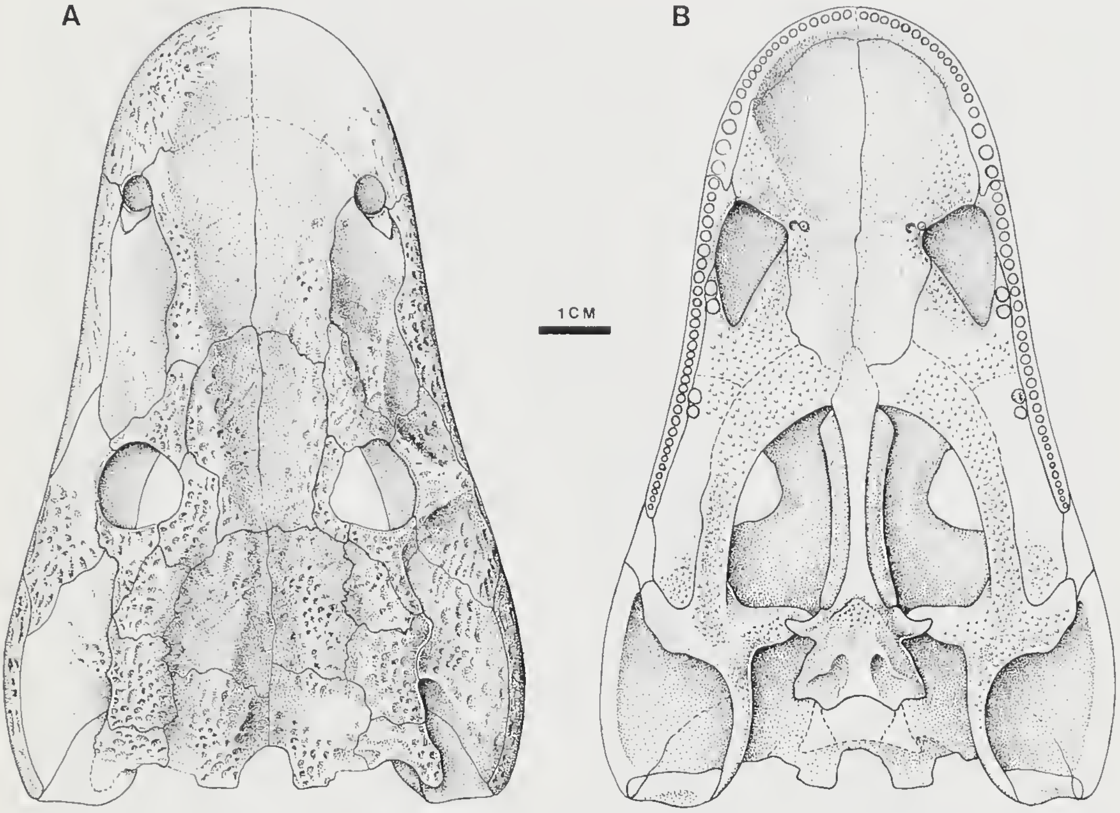
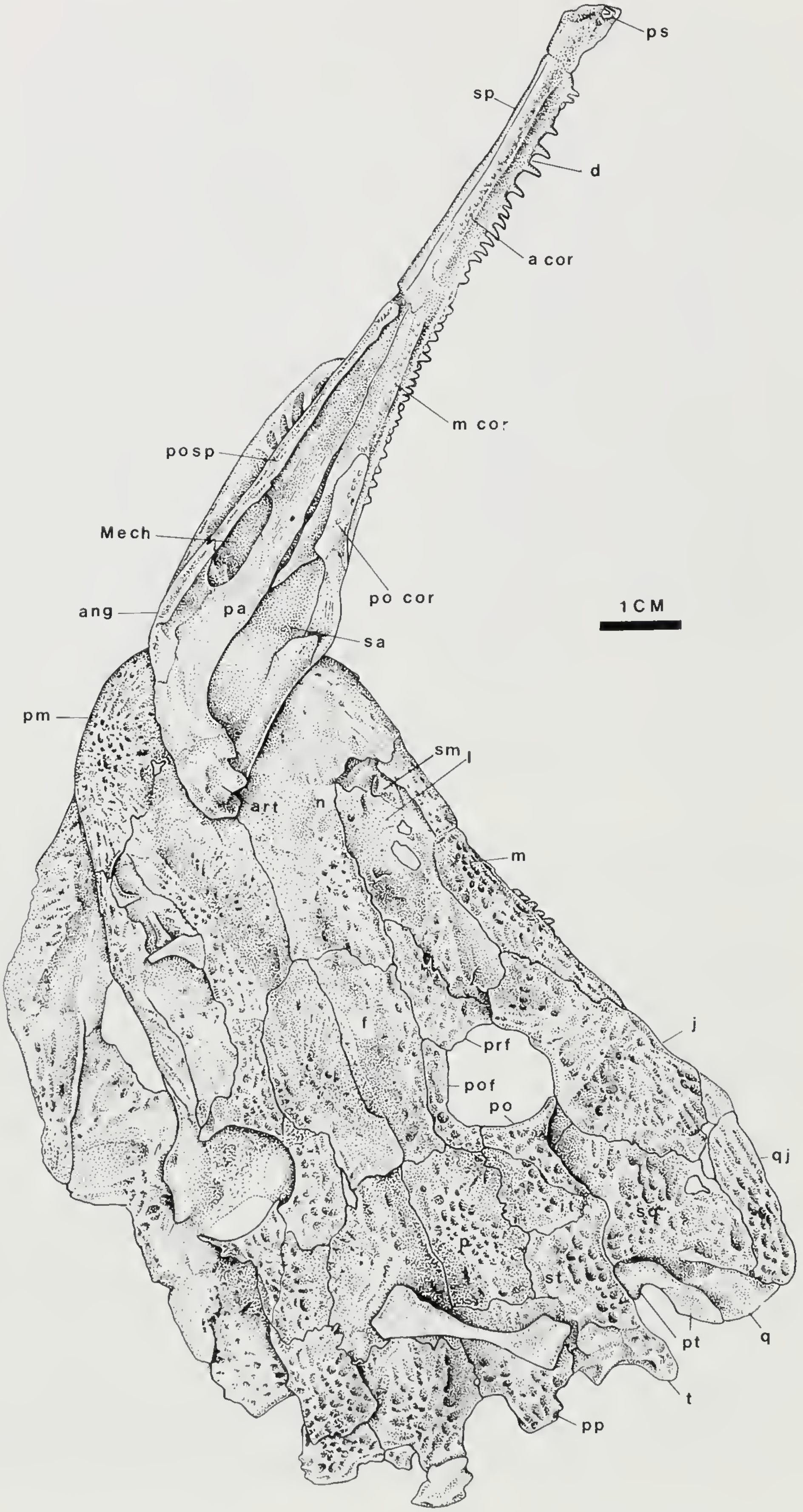


Figure 1. *Cochleosaurus florensis* Rieppel. Reconstruction of skull based largely on MCZ 4342 in A) dorsal view and B) ventral view.

of the premaxilla. Similar ridges are seen in the eryopoid temnospondyls *Zatrachys* (Langston, 1953), but unlike in the latter a deep longitudinal trough, nearly devoid of sculpturing, runs up the middle of the central depression, gradually becoming broader and more shallow as it passes anteriorly between the orbits onto the snout, where it terminates as an expansive, shallow depression between and anterior to the external nares. The lacrimal bears a low but distinct rounded ridge that passes anteroventrally across its surface. Anteromedial to the ridge, its concave surface bears only muted ornamentation, as in *Chenoprosopus* but in contrast to *C. bohemicus,* where no difference in texture occurs (personal observation). *Chenoprosopus* shows similar, sparsely ornamented depressions on the snout, but apparently not in the postorbital region (Langston, 1953).

The well-developed nasals equal the frontals in midsagittal length, but as in *Chenoprosopus,* the unusually long antorbital region is primarily formed by the remarkably large premaxillae,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which measure about 65% of the nasal length. Posterolaterally oriented nasopremaxillary sutures position the external nares well back from the tip of the snout. A less pronounced, but otherwise similar structure occurs in *Edops*. Large premaxillae and posteriorly positioned external nares also occur in the eryopoid *Zatrachys*, but the snout morphology is otherwise very different, and further comparisons are of doubtful value. The morphology of *Cochleosaurus* contrasts to that of long-snouted embolomeres such as *Archeria* (Holmes, 1989) in which the premaxillae are small and external nares are located anteriorly. Although the premaxillae are somewhat larger in *Archegosaurus* (Milner, 1978), it is primarily elongation of the frontals and in particular the nasals that account for the snout elongation and, unlike *Cochleosaurus*, the anterior margins of the elongate external nares are close to the anterior end of the snout. The posterior 6 of the approximately 20 premaxillary teeth gradually increase in size to form a pseudocanine peak just anterior to the premaxillary–maxillary suture. Large premaxillary teeth also occur in colosteids (Smithson, 1982) but comprise a tusk pair distinctly larger than the other teeth in a much smaller premaxilla. There is no marked size variation in the approximately 35 maxillary teeth except posteriorly, where they gradually become smaller.

The septomaxilla forms a posteriorly directed, apparently unornamented wedge on the dorsal surface of the snout. It nearly (right side of MCZ 4342) or completely (left side of MCZ 4342 and 4344) excludes the lacrimal from the margin of the external naris. In contrast to the condition in *Chenoprosopus*, a nasomaxillary contact is absent.

Variation in size and shape of some dermal elements occurs. The left postfrontal of MCZ 4342 is much wider than the right (Fig. 2). The postorbitals, although elongate and triangular in outline in most specimens (e.g., MCZ 4343 [Rieppel, 1980], MCZ 4344 [Fig. 3]), are significantly narrower posteriorly in MCZ 4342 (Fig. 2). The significance of this variation is unknown.

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Figure 2. *Cochleosaurus florensis* Rieppel. Specimen drawing of MCZ 4342 in dorsal view, showing right lower jaw in medial view.

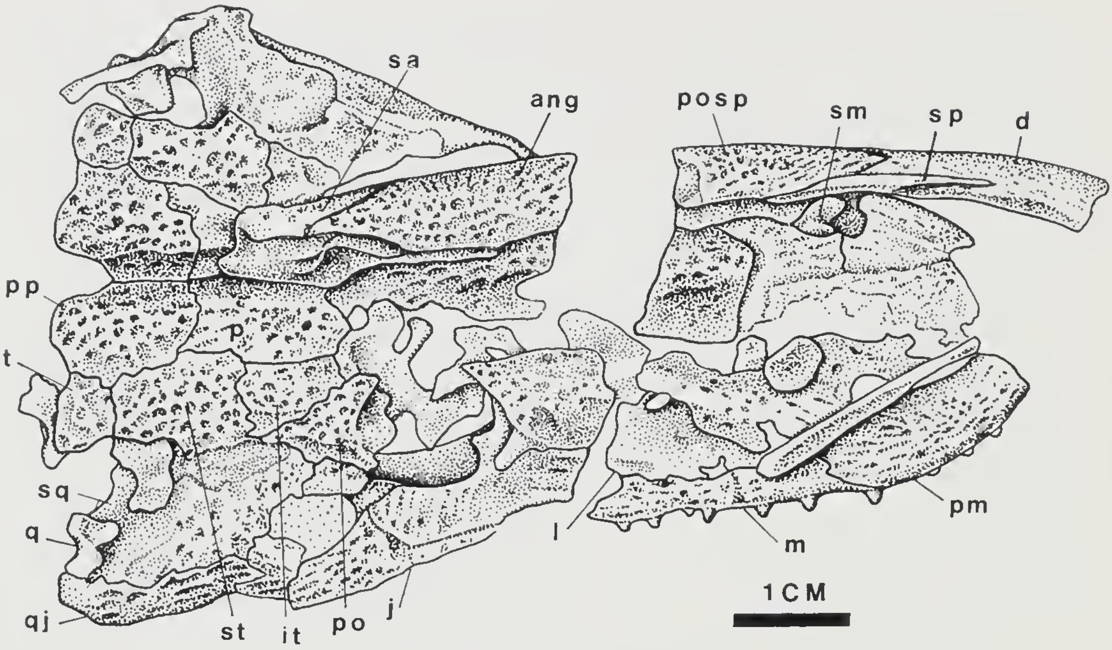

Figure 3. *Cochleosaurus florensis* Rieppel. Specimen drawing of MCZ 4344 in dorsal view, showing right lower jaw in ventral view.

The skull table in MCZ 4342, as in the type, is relatively wider than in *C. bohemicus.* A separate intertemporal is clearly present in all specimens. As in *Chenoprosopus,* the anterodorsal notch of the squamosal embayment reaches far forward along the edge of the table to the midpoint of the supratemporal. The latter bone thus forms a significant portion of the dorsal border of the embayment. This is distinctly different from the condition in other temnospondyls possessing embayments in which a posterodorsal process of the squamosal forms much of its dorsal border, severely limiting participation of the supratemporal or completely excluding it from the rim. The posterolateral corner of the right tabular in MCZ 4342 extends to form a blunt, triangular tabular "horn" that projects posteriorly and slightly ventrally. In contrast to the tabular horn of embolomeres (Panchen, 1970), it is not biramous and bears ornamentation on both dorsal and ventral surfaces. Prominent tabular projections, rare in temnospondyls, also occur in *Zatrachys*; however, they differ from those in *Cochleosaurus* in being posterodorsally curved, attenuated spikes that probably developed in association with the unique spiny ornamentation festooning the skull. Homologies with the tabular projections of other labyrinthodonts are doubtful. The "horn" is not as well developed in either MCZ 4343 (Rieppel, 1980), MCZ 4344 (Fig. 3), or any specimens of *C. bohemicus.* Such structures are often subject to positive allometry, but the horns are not particularly prominent in the largest specimen (MCZ 4343). The size of these horns is quite variable in *C. bohemicus* (Sequeira, personal communication), and this may also be the case in *C. florensis.* The postparietal lappets, although well developed in both specimens, are noticeably smaller than in equivalently sized *C. bohemicus.* They project straight posteriorly with their dorsal surfaces contiguous with that of the table rather than occupying a more ventral position on the occipital surface of the postparietal as in *Caerorhachis* or *Dendrerpeton.* Their ornamented dorsal surfaces are considered to be diagnostic for the genus (Sequeira and Milner, 1993).

Palate

The excellently preserved palate in MCZ 4342 (Fig. 4) bears denticles over much of the lateral portions of the vomers, the entire palatines, and ectopterygoids and most of the pterygoids except the posterodorsal part of the quadrate ramus. The snout is distinctly longer than described by Rieppel (1980), who based his reconstructions on the less well preserved palates of MCZ 4343 and 4344. Other than being broader, it is proportioned like that of *Chenoprosopus.* This elongation is produced by massive vomers, which account for about 45% of the snout–quadrate length in contrast to embolomeres (Panchen, 1970), other temnospondyls such as *Caerorhachis, Dendrerpeton* (Godfrey *et al.,* 1987), *Greererpeton, Edops,* and even the long-snouted *Archegosaurus* (Whittard, 1928), in which the vomers are relatively much shorter. Among temnospondyls, only *Neldasaurus* and the aberrant *Zatrachys* have vomers approaching these proportions. The triangular choanae, with their bases positioned anteriorly, occupy positions well posterior to the tip of the snout. Each vomer bears a small tusk and replacement pit at the apex of a pronounced triangular thickening located anteromedial to the choana. As in *Chenoprosopus,* a broad depression occupies the central portion of the plate between the anteriorly diverging medial margins of the thickenings.

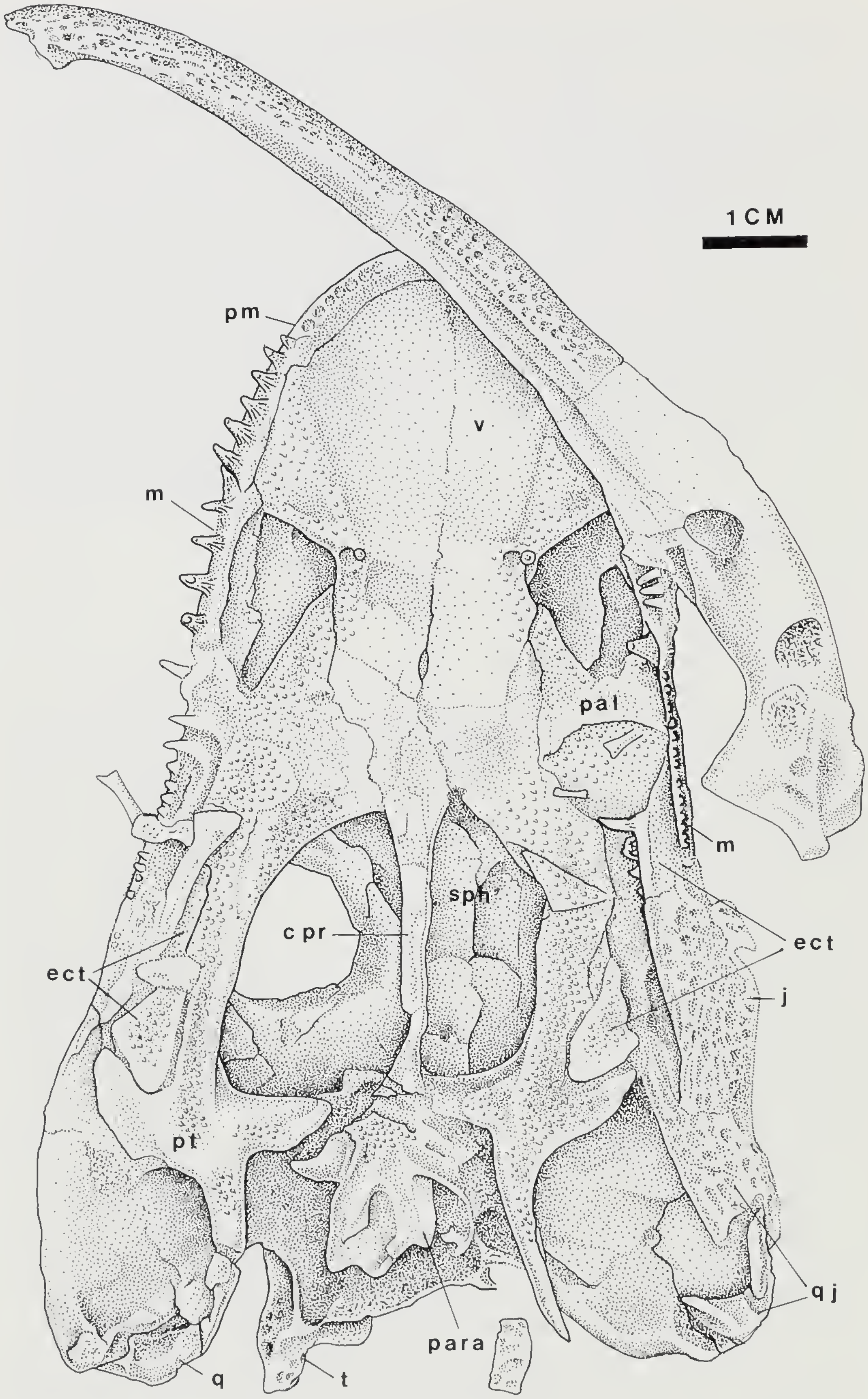
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TABLE 2. PROPORTIONS OF THE PALATE IN SOME EARLY TEMNOSPONDYLS: QUADRATE–ANTERIOR MARGIN OF THE INTERPTERYGOID VACUITIES/SNOUT–ANTERIOR MARGIN OF THE INTERPTERYGOID VACUITIES.*

Dendrerpeton acadianum (Godfrey *et al.*, 1987)	0.34
Greererpeton burkemorani (Smithson, 1982)	0.44
Edops craigi (Romer and Witter, 1942)	0.53
Cochleosaurus bohemicus (Steen, 1938)	0.59
Cochleosaurus florensis (Rieppel, 1980)	0.78
Chenoprosopus milleri (Langston, 1953)	0.84
Cochleosaurus florensis (this paper)	0.96
Caerorhachis bairdi (Holmes and Carroll, 1977)	0.61
Neldasaurus wrightae (Chase, 1965)	0.65

* 1.00 would indicate that the anterior margin of the interpterygoid vacuities lay equidistant between the snout and quadrate. These ratios are based on the restorations contained in the original publications.

The anterior borders of the modest interpterygoid vacuities are equidistant between the tip of the snout and quadrate condyles. In other early tetrapods, this margin is more anteriorly placed (Table 2).

The sutural outline of the palatine is difficult to follow, but its lateral extent is indicated by the presence of a palatine tusk and replacement pit clearly visible on the left side of MCZ 4342 immediately medial to the maxillary tooth row and lateral to the posterior corner of the choana.

In MCZ 4342, the left quadratojugal and posterior portion of the jugal have folded under the skull, exposing the lateral portion of the attached ectopterygoid and posterior portion of the maxilla. (Fig. 4). The concave dorsal surface of the displaced left ectopterygoid faces laterally, and the tusk pair—the anterior one complete, the posterior one missing the tip and overlaid by two small maxillary teeth—project medially. The region of the right ectopterygoid, where dentition might be expected, is obscured by an unidentified bone, possibly a hyoid element or limb bone.

←

Figure 4. *Cochleosaurus florensis* Rieppel. Specimen drawing of MCZ 4342 in palatal view, showing left lower jaw in ventral view.

Although the narrow palatal rami of the pterygoids almost certainly do not meet anteriorly, they contact the anterior end of the cultriform process, thus excluding the vomers from the rim of the moderate-sized interpterygoid vacuity. This morphology is here considered to be intermediate between the primitive temnospondyl condition in which the vacuities are completely bordered by pterygoids that meet anteriorly (*Caerorhachis, Greererpeton,* and *Edops*) and the more derived temnospondyl condition in which the vomers enter the margins of the vacuities (Milner, 1990a). This inferred evolutionary sequence is apparently correlated with an increase in the size of the vacuities. More posteriorly, the pterygoid projects laterally into the anterior portion of the opening of the subtemporal fossa, but no ventral deflection like that reported in *Chenoprosopus* is apparent.

A unique feature of the palate is the configuration of the pterygoid–ectopterygoid suture. In MCZ 4342, each pterygoid wraps around the roughly triangular posterior end of the ectopterygoid and extends a broad ala anterolaterally to form a relatively extensive contact with the inner surface of the jugal, thereby excluding the ectopterygoids and maxilla from the rim of the subtemporal fossa. In *Chenoprosopus,* a more modest lateral projection of the pterygoid forms a limited contact with the jugal. A point contact appears to occur in *Caerorhachis,* but indistinct sutures make this equivocal (Holmes and Carroll, 1977). A pterygoid–jugal contact also occurs in anthracosaurs (Panchen, 1970) and the saurerpetontid temnospondyl *Acroplous* (Foreman, 1990) but is accomplished by a medial process of the jugal (alary process) rather than by a lateral ala of the pterygoid. A pterygoid–jugal suture does not occur in other primitive amphibians such as *Greererpeton, Dendrerpeton, Edops,* loxommatids (Beaumont, 1977), and *Ichthyostega* (Jarvik, 1980).

In MCZ 4343, denticles extend beyond the basicranial articulation onto the quadrate ramus of the pterygoid (contra Rieppel, 1980, text-figs. 1, 2). The quadratojugal wraps around the posterolateral corner of the quadrate and appears to have made a modest contribution to the lateral portion of the quadrate condyle, although crushing makes it impossible to be certain.

Braincase

The braincase is much more completely preserved in MCZ 4342 (Fig. 4) than in either MCZ 4343 or 4344. The stout basipterygoid process inserts into a simple rectangular depression on the posteromesial margin of the remarkably stout basal process (Fig. 4, right side). Unlike *Greererpeton,* no evidence indicates a basal socket. The posterior lip of the cup-shaped distal end of the basipterygoid process wraps around the posterior margin of the basal process.

Between the basipterygoid processes is a conspicuously raised, triangular tubercle bearing a patch of denticles. The shape of this tubercle, consistent in both MCZ 4342 and 4343, distinguishes *C. florensis* from *Greererpeton* and *Caerorhachis,* where the tubercle is oval in outline. Lateral to the tubercle, an anteromedially directed groove, probably marking the course of the internal carotid and palatine arteries and nerves, crosses the base of each basipterygoid process.

The basal plate of the parasphenoid bears two V-shaped depressions, the "tubera basisphenoidales" (Romer, 1930; Smithson, 1982), the lateral margins of which are bordered by prominent crests. The smooth periosteal floor of each pocket and the low median ridge that separates them extend to the posterior margin of the parasphenoid.

The cultriform process in MCZ 4342 becomes progressively broader anterior to the midpoint of the interpterygoid vacuities (contra Rieppel, 1980). In many early temnospondyls such as *Caerorhachis, Greererpeton,* and *Edops,* the process remains approximately parallel-sided or may even narrow anteriorly. However, an anteriorly expanded process is present in a range of temnospondyls such as *Dendrerpeton* (Godfrey *et al.,* 1987), *Neldasaurus,* and *Zatrachys,* making the significance of this feature unclear. Anteriorly, the process forms a broad wedge between the pterygoids and appears to contact the vomers, but lack of well-defined sutures makes this difficult to confirm (Figs. 1B, 4).

A well-ossified sphenethmoid is exposed through the left interpterygoid vacuity of MCZ 4342 (Fig. 4). During dorsoventral compression of the skull, it was rotated to expose its featureless left lateral surface. It extends anteriorly almost to the front of the interpterygoid vacuity. Its rear margin is obscured by the basal process.

The otico-occipital portion of the braincase of MCZ 4342 has been crushed against the ventral surface of the skull, obscuring its morphology.

Lower Jaw

The mandible, which bears no lateral line sulci, is particularly slender anteriorly (Fig. 5). The right half, exposed in a medial view (Fig. 4), is crushed, but complete. A parasymphyseal tusk is present. There is no canine peak, although the teeth in the anterior half of the tooth row are somewhat larger. Each dentary could have held at least 55 labyrinthine-infolded teeth.

Three denticle-covered coronoids form most of the dorsomedial surface of the jaw anterior to the adductor fossa. MCZ 4342 preserves what appears to be a coronoid–surangular suture on the medial surface of the outer wall of the adductor fossa. A coronoid contribution to the surangular crest, present in some derived temnospondyls like *Tersomius* (Carroll, 1964) and *Phonerpeton* (Dilkes, 1990), would represent a derived condition relative to primitive tetrapods such as *Caerorhachis, Greererpeton,* and *Edops* in which the posterior coronoid does not contribute to the surangular crest, but its level of apomorphy remains uncertain. In MCZ 4342, however, the usually straight course of the proposed "suture" suggests that it may be a break, and a distinct change in texture of this element at the anterior end of the adductor fossa provides an alternate position for the coronoid–surangular suture. Medially, the posterior coronoid forms the anterodorsal rim of the adductor fossa and then extends to a rounded termination anteriorly. The long, narrow anterior coronoid can be distinguished from the dentary dorsally and presplenial ventrally, but the sutures become obscured toward the symphysis. The limits of the middle coronoid are problematic. Although it is easily distinguished from the dentary dorsally and prearticular ventrally, its anterior suture is obscured by broken bone surface. Posteriorly, it appears to pass ventral to the posterior coronoid to form part of the ventrolateral margin of the adductor fossa (Fig. 4), a unique

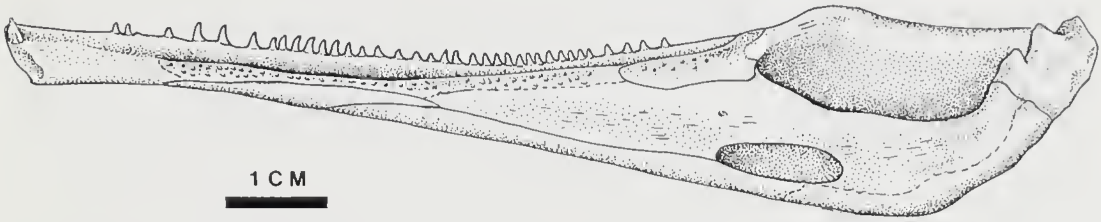

Figure 5. *Cochleosaurus florensis* Rieppel. Reconstruction of lower jaw in medial view, based primarily on MCZ 4342 with additional information from MCZ 4344.

condition for early tetrapods. However, the bone surface of this apparent posteroventral extension bears a much closer resemblance to that of the adjacent prearticular, suggesting that the latter has been broken into two longitudinal splints. A conservative reconstruction of the coronoids is presented here (Fig. 5), although the alternative interpretations already discussed cannot be dismissed unequivocally.

A broadly rounded ridge, visible on the dorsal portion of the medial surface of the surangular, extends from its suture with the posterior coronoid to the mandibular condyle.

There is a relatively large Meckelian fenestra at the common junction of the prearticular, postsplenial, and angular. Crushing makes it impossible to confirm the presence of more anterior fenestrae.

The right ramus of MCZ 4344, preserved in ventral view, allows the mutual relationships of the angular, articular, surangular, and splenials to be determined (Fig. 3). The large, coarsely sculptured angular, occupying the posterior one-third of the ramus, forms a suture posteriorly and dorsally with the surangular. The latter is not exposed on the medial surface of the ramus, which is formed in this region by a lamina of the articular (Fig. 3). A reexamination of MCZ 4343 confirms this (contra Rieppel, 1980, text-figs. 1, 2). A 1-cm section is missing from the middle of the ramus of MCZ 4344, which otherwise is undisturbed. The dentary forms a broad contact posteriorly with a large postsplenial (splenial) that has an extensive, coarsely sculptured lateral exposure. A much smaller, splint-like splenial (presplenial) with only ventral and medial exposure and muted sculpturing occupies a position between these two elements. Reexamination of MCZ 4343 indicates that the "angular" as described by Rieppel (1980) is actually the angular and postsplenial separated by a cryptic suture. Consequently, the suture pattern in this area conforms to the primitive temnospondyl pattern (e.g., *Dendrerpeton, Greererpeton, Edops, Neldasaurus*), and an angular-splenial (presplenial) contact does not occur. This putative character was thought to be shared with *Chenoprosopus* (Rieppel, 1980). Langston (1953:369) clearly indicated that the ". . . intersplenial sutures are not clear . . . ," raising the possibility that his "angular" (Langston, 1953, text-fig. 6) is, like the angular as described by Rieppel, a compound element. If this is the case, then *Chenoprosopus* would also conform to the primitive pattern.

Denticles are absent on the prearticular. The articular lacks a retroarticular process.

DISCUSSION

The information provided by MCZ 4342 and 4344 allows a more precise diagnosis of *Cochleosaurus florensis* and the family Cochleosauridae. An initial attempt is made to establish the polarity of characters discussed below by accepting the reasonable hypothesis (Milner, 1990b) that the primitive character states for the Temnospondyli are exhibited by dendrerpetontids, edopsids, and trimerorhachoids. *Dendrerpeton, Edops,* and *Neldasaurus* are used for this purpose. Where data are missing or inconsistent, interpretation is equivocal, or relationships above the family level are discussed, the more distantly related *Caerorhachis, Greererpeton,* loxommatids, embolomeres, and *Ichthyostega* are used as outgroups.

Rieppel (1980) used the following characters to distinguish *Cochleosaurus florensis* from *C. bohemicus*: 1) smaller adult size, 2) shorter postparietal lappets, 3) wider skull table, 4) smaller orbits, and 5) shorter snout. To support the character of smaller size, he argued that in contrast with *C. bohemicus* the uniformly rounded pitting on the skull roof of the type of *C. florensis* indicated that maximum adult size had been reached (Bystrow, 1935). Although some elements of MCZ 4342 and 4344 bear elongate pits toward their edges, indicating that rapid growth was still occurring at the time of death, they are far less developed than in larger specimens of *C. bohemicus* and so tend to support his original hypothesis, albeit not as strongly. Both MCZ 4342 and 4344 confirm the presence of smaller postparietal lappets in *C. florensis.* The skull table in MCZ 4342, as in the type, is wider than that of *C. bohemicus,* and this condition probably represents a valid distinction. The much smaller size of MCZ 4344 makes the reliability of such comparisons dubious. The status of the remaining characters is equivocal. The orbits of MCZ 4342 are distinctly smaller than an equivalent-sized *C. bohemicus,* but a reexamination of the type reveals an orbital diameter of about 18 mm after correcting for crushing (contra Rieppel, 1980), within the range expected for *C. bohemicus.* The well-preserved vomers of MCZ 4342 indicate that the snout of *C. florensis* is longer than estimated on the basis of the distorted type, exhibiting proportions similar to those of *C. bohemicus.* The unusually well-developed lateral ala of the pterygoid that wraps around the V-shaped posterior extremity of the ectopterygoid to form an extensive contact with the jugal may constitute an additional diagnostic feature, but the detailed morphology of this region has not been described in *C. bohemicus.* Although it appears probable that the Florence material represents a distinct species, more detailed comparisons await publication of a description of *C. bohemicus* presently being prepared by Sandra Sequeira at Birkbeck College, London.

The Cochleosauridae

Four genera are presently included in the family Cochleosauridae: *Cochleosaurus, Chenoprosopus,* and the poorly known *Gaudrya* and *Macrerpeton* (Carroll, 1977, 1988). The type of *Gaudrya* (Fritsch, 1885), comprising the anterior end of a snout, has been synonymized with *Cochleosaurus bohemicus* (Sequeira and Milner, 1993), making *Gaudrya* its junior synonym. Two specimens from Linton, Ohio (AMNH 2933 and 6954), originally assigned to *Leptophractus* by Romer (1930) but later transferred to *Gaudrya* on the basis of close similarities in palatal structure to the type (D. Baird, personal communication) should therefore also be reassigned to *Cochleosaurus.* Other specimens referred to *Gaudrya* (Romer, 1947) are not cochleosaurids (A. R. Milner, personal communication). The poorly known *Macrerpeton,* presently being studied by Robert Hook, appears to be a derived cochleosaurid, but until a thorough review of its anatomy is completed more specific relationships cannot be established.

Members of the family Cochleosauridae share the following derived features:

1. Absence of parietal foramen and lateral line sulci.
2. Elongate, triangular choanae wider anteriorly than posteriorly.
3. Squamosal lacking posterodorsal process, leaving much of the lateral edge of the supratemporal exposed along the anterodorsal margin to the squamosal embayment.
4. Lateral ala of the pterygoid contacts the jugal to exclude the ectopterygoid and maxilla from the rim of the subtemporal fossa.

In addition, all cochleosaurids share at least two features that, although probably homologous, are problematic:

5. Large premaxillae with posterolaterally directed nasal sutures, resulting in posteriorly positioned external nares. Although not developed to the same degree, this snout configuration also occurs in *Edops,* and may diagnose the more inclusive superfamily Edopoidea (see later).
6. Extreme elongation of the premaxillae and vomers, producing an elongate preorbital region and posterior position of both external and internal nares. Enlarged vomers also occur in *Archegosaurus* and *Zatrachys.* In the former, however, the anterior borders of the choanae are much closer to the front of the snout, and there is no comparable development of the premaxillae. In the latter, the circular choanae are posterior in position, but the highly derived palatal structure of this aberrant eryopoid makes further comparisons difficult.
7. System of prominent, rounded ridges on the skull roof separating depressed areas exhibiting muted sculpturing. Although this striking set of features allows one to immediately distinguish cochleosaurs from other Carboniferous tetrapods, it is not unique to the family. The distantly related Permian eryopoid *Zatrachys* bears a similar system of ridges and depressions (Langston, 1953). However, direct comparison is difficult

because in *Zatrachys* a large fenestra occupies the region of the snout bearing the bowl-shaped depression in cochleosaurs, and in contrast to cochleosaurs the other depressions on the dermatocranium appear to bear well-developed ornamentation. Although this is probably a convergent feature, its occurrence in at least one other temnospondyl family renders it unreliable for establishing relationships.

Differences between *Cochleosaurus* and *Chenoprosopus*

Some of the differences between *Cochleosaurus* and *Chenoprosopus* are essentially proportional and arguably correlated with the smaller size of the former (with a skull of one-half to one-third the length of the latter). Although they serve to distinguish the known specimens of these two taxa, their status as diagnostic characters is uncertain. These include the following:

1. A longer snout in *Chenoprosopus* relative to that of *Cochleosaurus,* with a ratio of antorbital length (measured from the midpoint of the orbit) to postorbital length (measured to the posterior edge of the postparietal lappet) of 2.0 in the former and 1.5 in the latter.
2. A more narrowly parabolic skull outline in *Chenoprosopus* with a maximum skull length-to-width ratio of 1.9 as compared to 1.6 in *Cochleosaurus.*
3. A relatively longer, more posteriorly projecting suspensorium in *Chenoprosopus.*
4. Contact between the septomaxilla and lacrimal reduced or absent in *Chenoprosopus,* resulting in a nasomaxillary contact. This also occurs in the long-snouted *Archegosaurus* (Milner, 1978) and the trimerorhachoid *Neldasaurus.*

Other differences, not obviously size-related, are considered as derived features of *Chenoprosopus.* These include the following:

5. Prominent, denticle-bearing ridges present on the vomers, pterygoids, palatines, and ectopterygoids.
6. Basicranial articulation apparently sutured and immobile in adults. This also occurs in most eryopoid temnospondyls but it not considered characteristic of edopoids (Carroll, 1988).

7. Ventral surface of the cultriform process bearing a string of denticles.
8. Vomerine pits (Sequeira and Milner, 1993).

The Edopoidea

The generally plesiomorphic status of the Cochleosauridae has prompted most authors to place the family near the base of temnospondyl phylogeny, traditionally comprising, with the Edopidae, the superfamily Edopoidea (e.g., Carroll, 1988). However, no undisputed synapomorphies have been identified. This has resulted in different interpretations of relationship between the Edopidae and Cochleosauridae, including sister-group relationship within a monophyletic Edopoidea (Milner, 1990a), structural grade (Trueb and Cloutier, 1991), and distant relationship, with each family included within distinct groups of temnospondyls (Boy, 1990).

A reassessment of the Edopoidea is beyond the scope of this paper, but a few comments are appropriate. Boy (1990), in a phylogenetic analysis of European Lower Permian temnospondyls, argued against a close relationship between *Edops* and *Chenoprosopus,* instead hypothesizing a sister-group relationship between the latter and the clade *Archegosaurus* + *Sclerocephalus* based on the following characters: 1) nasomaxillary suture, 2) elongate, anteriorly constricted prefrontal, and 3) pterygoid (?read parasphenoid)–vomer contact. However, all three characters are correlated with the elongation and narrowing of the snout. A nasomaxillary suture also occurs in the relatively long-snouted *Neldasaurus.* Although not an inevitable correlate of snout elongation, it could be expected to occur in any skull exhibiting rapid anteroposterior growth of the nasal and/or premaxilla relative to the lacrimal. A comparable prefrontal morphology is seen in the similarly proportioned but clearly unrelated *Archeria* (Holmes, 1989), and, as Boy pointed out, the pterygoid (?read parasphenoid)–vomer contact arises independently in most other genera included in his analysis (Boy, 1990, fig. 9).

Sequeira and Milner (1993) hypothesized a monophyletic Edopoidea based on the presence of enlarged premaxillae that form a long common medial suture and extend far posteriorly along the jaw margin behind this median suture, bordering small inset external nares. Unlike the characters used by Boy (1990), this represents a unique form of snout elongation in which the premaxillae account for most of the increased preorbital length and is here considered more reliable for establishing relationships. The anatomy of *Cochleosaurus florensis* supports this hypothesis. The occurrence of the prefrontal–jugal contact excluding the lacrimal from the orbit, although probably derived within the group, is correlated with snout elongation and found in other groups (e.g., embolomeres) and is of less certain value.

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A NEW LIZARD OF THE GENUS *MACROPHOLIDUS* (TEIIDAE) FROM A RELICTUAL HUMID FOREST OF NORTHWESTERN PERU, AND NOTES ON *MACROPHOLIDUS RUTHVENI* NOBLE

JOHN E. CADLE[1,3] AND PABLO CHUNA M.[2]

ABSTRACT. *Macropholidus ataktolepis,* new species, is a microteiid lizard known only from the type locality, Bosque Cachil, in the western Andes of extreme southwestern Cajamarca Department, Peru. It differs from the only other species of the genus, *Macropholidus ruthveni* Noble, in having prefrontal scales and in having the paired series of enlarged dorsal scales disrupted at or before midbody, rather than continuing to the tail. In addition, taxonomic data and natural history observations for *M. ruthveni* are summarized, including data for a large sample from the Rio Zaña valley of northwestern Peru (Cajamarca Department).

RESUMEN. *Macropholidus ataktolepis,* nueva especie, es un microtéido conocido solamente en la localidad típica, Bosque Cachil, en los Andes occidentales del extremo suroeste del departamento de Cajamarca, Perú. La nueva especie difiere de *Macropholidus ruthveni* Noble, la única otra especie del género, por tener escamas prefrontales y tener la serie pareada de escamas dorsales agrandadas disruptidas hasta o antes de la mitad del cuerpo, antes que continuar hasta la cola. Además, se resumen datos taxonómicos y observaciones de la historia natural para *M. ruthveni,* incluyendo datos para una muestra grande de esa especie procedente del valle del Río Zaña al noroeste del Perú (Departamento de Cajamarca).

INTRODUCTION

As a result of recent explorations, the Andean slopes of northwestern Peru continue to yield many new species of amphibians and reptiles (Cadle, 1989, 1991; Cadle and McDiarmid, 1990; Duellman and Wild, 1993). In addition, distributions of species

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previously known from few localities in this region are being refined. Most of the new discoveries have come from remnants of mesic to humid forests that occur in scattered patches on the western slope of the Andes from the Ecuadorian border to central Peru (H. W. Koepcke, 1957, 1961; H. W. Koepcke and M. Koepcke, 1958; M. Koepcke, 1954). These forests are thus islands in the sea of arid mountainous terrain characteristic of this portion of western South America. This paper describes a small lizard recently discovered in one such forest remnant and provides additional data on its presumed closest relative, *Macropholidus ruthveni* Noble. *Macropholidus ruthveni* proved to be common at Bosque Monte Seco, another forest isolate in the Rio Zaña valley just north of the type locality of the new species and from which other species of frogs, lizards, and snakes have been recently described (Cadle, 1989, 1991; Cadle and McDiarmid, 1990).

Noble (1921a) erected the genus *Macropholidus* for a species of microteiid lizard (type species, *M. ruthveni*) from the "cordillera forming the boundary between the Departments of Piura and Cajamarca [Peru]." He compared *Macropholidus* only to *Pholidobolus,* a genus of the Ecuadorian Andes, from which *Macropholidus* was distinguished by (1) its possession of two enlarged, smooth, hexagonal rows of medial dorsal scales, the character that provided the etymology for the generic name, and (2) the lack of reduced scales laterally on the body. *Macropholidus ruthveni* has, until now, been known from only the four specimens in the type series. Subsequently, Parker (1930) described *Macropholidus annectens* from the vicinity of Loja City, Ecuador, and noted that this species shared scutellational characters with both *Macropholidus* and *Pholidobolus.* In particular, *M. annectens* lacked the enlarged dorsals characteristic of *M. ruthveni* but, instead, had dorsal scales similar to some species of *Pholidobolus.* Montanucci (1973) transferred *annectens* to *Pholidobolus* but retained *Macropholidus* as a monotypic genus characterized by the enlarged dorsals, a feature not seen in *Pholidobolus* (Montanucci, 1973:5). Other than Montanucci's brief discussion, *Macropholidus* has rarely been mentioned in the literature subsequent to Parker's description of *annectens.* Some workers (e.g., Presch, 1980) treated the two genera as synonymous based on a consideration of *annectens,* which is much better known than *ruthveni,*

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the type species of *Macropholidus.* The new species described herein has the enlarged dorsals characteristic of *Macropholidus,* but they do not form as extensive a series as in the type species, *M. ruthveni.*

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MATERIALS AND METHODS

The type series of the new species consists of nine specimens. The type series ($N = 4$) of *Macropholidus ruthveni* was also examined, as well as a series ($N = 24$) of that species recently collected by the senior author from the Rio Zaña valley, southwestern Cajamarca Department, Peru, and one other specimen referred to *ruthveni* from a locality (Lima Department) far south of the other known localities for that species. Details on these samples are given in the section on *ruthveni,* later.

Snout–vent length (SVL; the straight line distance from the tip of the snout to the vent) and tail length (TL; vent to tip of tail, regenerated portion separated by a + sign) were measured to the nearest 0.5 mm with a metric ruler. All other measurements were taken to the nearest 0.1 mm with dial calipers: head length (HL; tip of snout to posterior margin of ear), maximum head width (HW) and depth (HD), and body length (BL; posterior margin of arm to anterior margin of leg).

The terminology of scales in lizards generally is difficult to standardize; we used Peters (1964) and Smith (1946:17–30) as guides herein. Most of the potentially confusing scale terminology concerns the circumorbital series and the series of scales on the ventral surface of the head. Definitions used herein are the following: *Superciliaries* include scales contacting the supraorbitals and at least one-half of whose area is dorsal to the orbit. *Genials* are large paired scales posterior to the postmental, in contact on the midline and contacting the infralabials laterally. *Postgenials* are enlarged scales posterior to the genials, in contact laterally with the infralabials and not in contact medially. *Gulars* are scales enclosed by the genial–postgenial series anteriorly and the gular fold posteriorly; in *Macropholidus,* the gular series includes a paired series of enlarged medial gular scales extending anteriorly from the gular fold as well as smaller scales between the enlarged series and the genial–postgenial series. *Dorsals* are considered to be all scales on the trunk except for the squarish ventral plates;

this definition includes "laterals" as defined by Smith (1946:27). In *Macropholidus,* the middorsal pair of dorsal scales is considerably enlarged (*medial dorsals*). *Paradorsals* are a pair of scale rows, somewhat larger than other dorsals, that border the medial dorsal rows.

Transverse dorsal scale rows were counted from the occipitals to the posterior margin of the hindlimb. Transverse ventrals were counted between the limbs (axilla to groin). Counts of subdigital lamellae included the terminal claw sheath.

Museum abbreviations for specimens referred to are Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History, New York (AMNH), Field Museum of Natural History, Chicago (FMNH), University of Kansas Museum of Natural History (KU), and Museum of Comparative Zoology, Harvard University (MCZ). Specimens of *Macropholidus ruthveni* referred to only by J. E. Cadle field numbers (JEC) will be deposited in the Museo de Historia Natural de San Marcos, Lima.

DESCRIPTION

Macropholidus ataktolepis, new species

Figures 1, 3, 4

Holotype (Figs. 1, 3, 4). MCZ 178050 (field number JEC 10320), an adult female collected by Pablo Chuna Mogollon, 28 September 1991, at Bosque Cachil, approximately 3 km (airline) SE Contumazá, 2,400 m, Cajamarca Department, Peru (07°23′S, 78°47′W; Fig. 2).

The type locality (Fig. 2) is the site of ongoing biological surveys by Abundio Sagástegui, Pablo Chuna, and their colleagues of the Universidad Antenor Orrego, Trujillo, Peru. It lies in a small montane valley near the main road between Cascas and Contumazá in extreme southwestern Cajamarca Department.

Paratopotypes. The following eight specimens, all collected at the type locality: MCZ 178038–39 collected 27 July 1993 by P. Chuna M., P. Lezana, and S. Leiva; MCZ 178045–46 collected 17 May 1993 by P. Chuna M. and P. Lezana; and MCZ 178264–67 collected 12 December 1993 by P. Chuna M.

Etymology. The species name, a noun in apposition derived from the Greek *ataktos* (disordered, irregular, not arranged) +

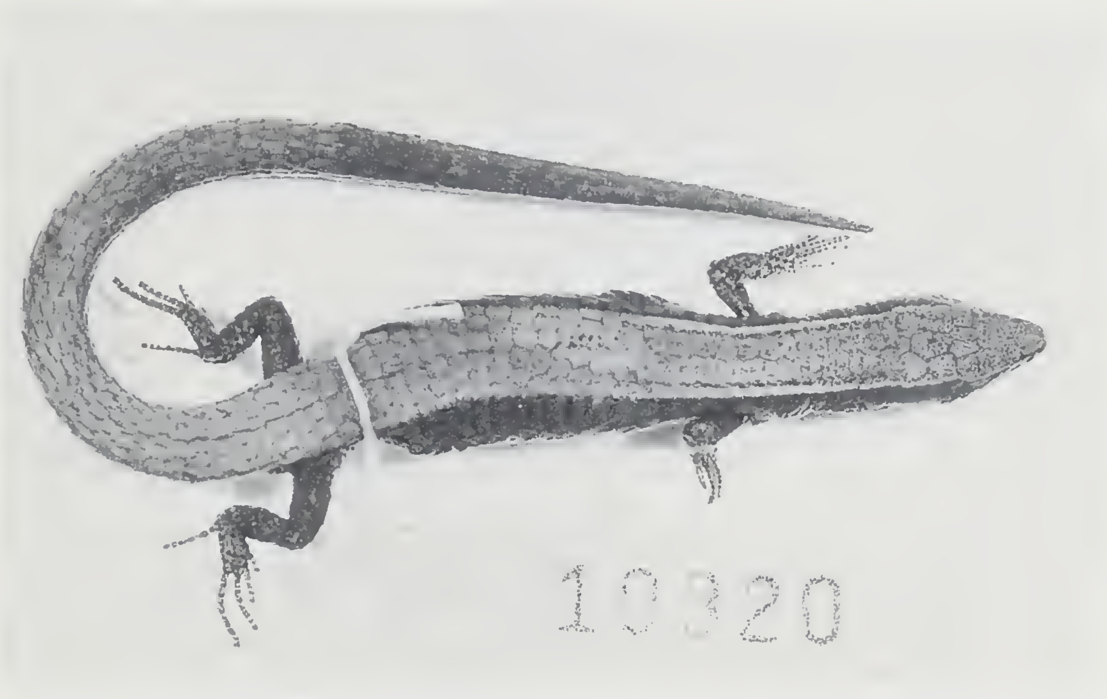

Figure 1. The female holotype of *Macropholidus ataktolepis* (MCZ 178050) in dorsal view.

lepis (scale), alludes to the disruption of the orderly array of enlarged dorsal rows in this species, as compared to the completely regular series in the type species of the genus.

Diagnosis. Macropholidus ataktolepis differs from the only other species of the genus, *M. ruthveni,* in having (1) a pair of prefrontal scales (absent in *ruthveni*); (2) the paired series of enlarged middorsal scale rows continuous only on the anterior part of the body (continuous to, or nearly to, the tail base in *ruthveni*); and (3) a regular arrangement of four enlarged temporal scales (irregular in number [1–7] and arrangement in *ruthveni*). *Macropholidus ataktolepis* differs from *Pholidobolus* (formerly *Macropholidus*) *annectens* (Parker) in having prefrontal scales and a double row of enlarged medial dorsal scales on the anterior part of the body. No species of *Pholidobolus,* as currently defined (Montanucci, 1973), has a double row of enlarged medial dorsals (see additional comments later).

Description (Type Series). The type series comprises the female holotype (38.5 mm SVL) and the following paratypes: four males (MCZ 178038–39, 178265–66; 29–35 mm SVL); two females (MCZ 178045, 178264; 39–43 mm SVL); and two juveniles (MCZ

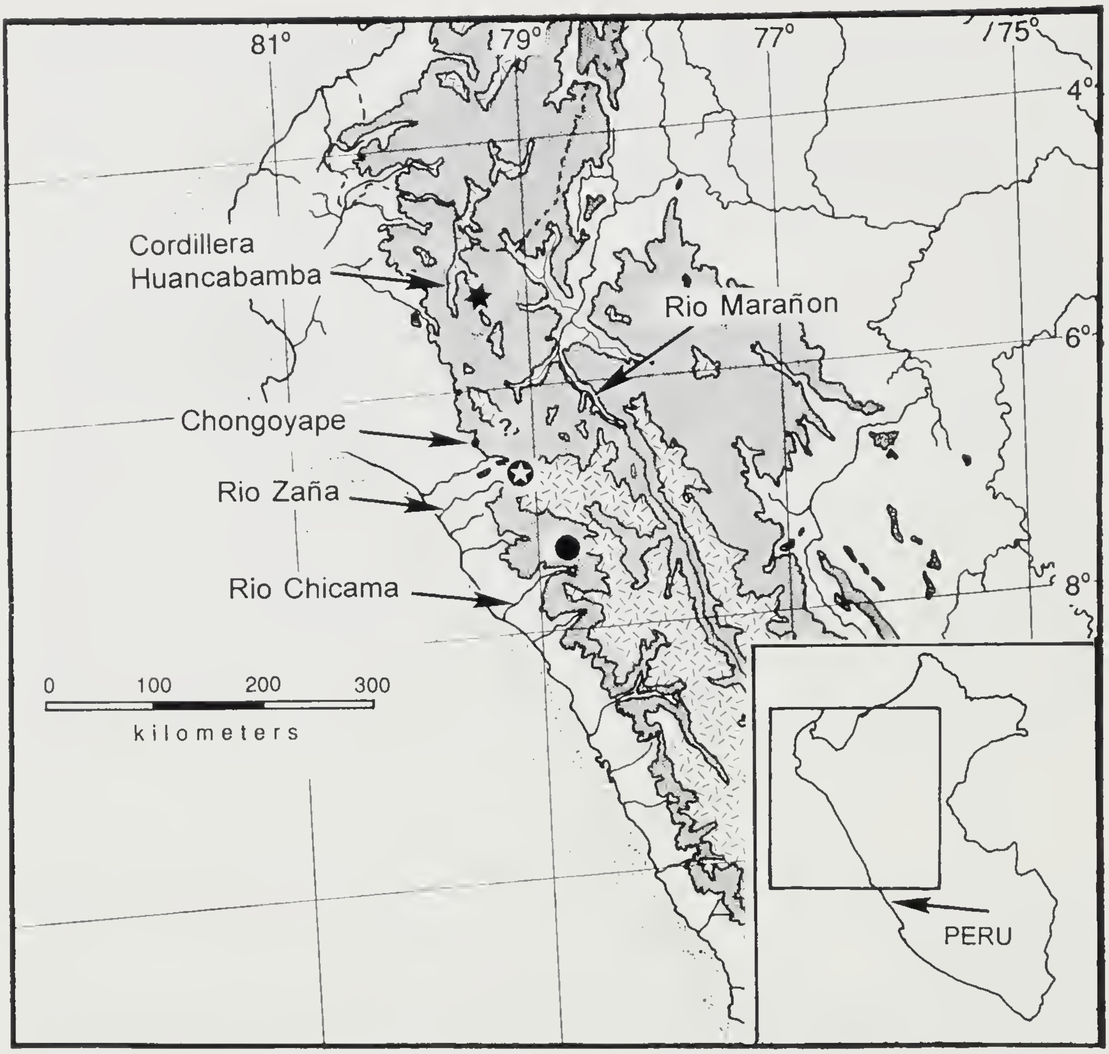

Figure 2. The Andes of northwestern Peru showing distributions of species of *Macropholidus*, place names, and physical features. Stippled area is above 1,000 m; hatched area is above 3,000 m. Star marks the type locality of *M. ruthveni*. Star within circle is the other known locality for *M. ruthveni*, Bosque Monte Seco (Cajamarca Department). Dot marks the type locality for *M. ataktolepis*, Bosque Cachil (Cajamarca Department). The question mark in northern Peru denotes the possible approximate locality for the "Chongollapi" paratypes of *ruthveni* (see text). The arrow within the inset map shows the location of Chaclacayo (Lima Department), from which comes an enigmatic specimen provisionally referred to *M. ruthveni* (KU 220845; see text).

178046, 178267; 19.5–22 mm SVL). Thus, adult females attain a larger size than adult males. Measurements and scale counts of the holotype are given in Table 1, and meristics and proportional data are given for the series in Table 2.

HL 21–24% SVL in adults (28% in juveniles), 1.5–1.9 times longer than wide, 1.3–1.7 times wider than high. Head slightly

TABLE 1. MEASUREMENTS (IN MILLIMETERS) AND SCALE COUNTS FOR THE HOLOTYPES OF *MACROPHOLIDUS ATAKTOLEPIS* AND *MACROPHOLIDUS RUTHVENI*.

	ataktolepis Holotype, MCZ 178050, Female	*ruthveni* Holotype, MCZ 14041, Female
Snout–vent length	38.5	45.5
Tail length	32 + 24	34 + 37
Head length	8.2	9.6
Head width	4.8	5.5
Head depth	3.2	3.4
Body length	20.3	26.1
Scales around midbody	19	19
Subdigital lamellae, finger IV	13, 14	16, 16
Subdigital lamellae, toe IV	16, 16	19, 18
Total transverse dorsal rows	31	33
Total enlarged medial dorsal pairs	15	30
Transverse ventrals between limbs	21	21

wider than neck, which is as wide as anterior body. Body cylindrical, slightly depressed. Complete tail in adults greater than twice SVL (2.1 times SVL in MCZ 178045 with tail tip missing, 2.4 times SVL in MCZ 178038 with complete tail); 68% and 70% of total length in these two specimens, respectively. Tail squarish to oval in cross section at base, tapering toward tip. Limbs pentadactyl, with well-developed digits; all digits with terminal claws. Forelimb extended forward along neck and head reaches posterior border of eye, or slightly anterior to this. Tongue (examined in MCZ 178045) lanceolate, covered with thin, scale-like papillae arranged in oblique rows, tip bifid; 8/8 heavily pigmented infralingual plicae. Anterior teeth conical, posterior teeth laterally compressed, tricuspid.

Head. Head short, depressed (depth 58–79% of width); snout blunt (Figs. 1, 3). Rostral wider than deep, visible from above, laterally in contact with first supralabial and anterior nasal, dorsally in contact with frontonasal. Frontonasal pentagonal, with slightly curved anterior border and obtusely pointed posterior border, separating nasals; posterolaterally narrowly contacting loreal (MCZ 178039, 178045–46, 178050, 178264–67) or narrowly separated from it by prefrontal–posterior nasal contact (MCZ

Table 2. Scale counts, measurements, and ratios for populations of *Macropholidus ataktolepis* and *M. ruthveni*. Values are means ± 1 standard deviation; ranges in parentheses. Sample sizes for scale counts are given at the head of each column; for body proportions, juveniles were not included in the calculations, and sample sizes for these are given adjacent to the ranges. Ranges for snout–vent lengths (SVLs) are given separately for each sex and unsexed juveniles.

	Macropholidus ataktolepis, Bosque Cachil (*N* = 9)	*Macropholidus ruthveni*, Bosque Monte Seco (*N* = 24)	*Macropholidus ruthveni*, Coucumayo (*N* = 2)	*Macropholidus ruthveni*, "Chongollapi" (*N* = 2)
Transverse ventrals	20.9 ± 0.60 (20–22)	20.9 ± 0.86 (19–22)	20.0 ± 1.0 (19–21)	20 (AMNH 38818)*
Transverse dorsals	32.8 ± 1.92 (29–35)	34.1 ± 1.17 (32–37)	33.5 ± 0.5 (33–34)	33.5 ± 1.5 (32–35)
Enlarged medial dorsal pairs	15.3 ± 2.74 (12–20)	30.8 ± 2.15 (25–35)	28.0 ± 1.0 (27–29)	33.0 ± 2.0 (31–35)
Total dorsal rows–enlarged dorsal rows	17.4 ± 3.7 (12–22)	3.29 ± 1.79 (0–7)	5.5 ± 1.5 (4–7)	0.5 ± 0.5 (0–1)
Scales around midbody	19.7 ± 0.71 (18–20)	19.4 ± 0.70 (17–20)	19.0 (19)	18.5 ± 0.5 (18–19)
Subdigital lamellae, finger IV	13.2 ± 0.67 (12–14)	12.9 ± 0.88 (11–14)	14.5 ± 1.5 (13–16)	13.0 (13)
Subdigital lamellae, toe IV	17.6 ± 1.13 (16–19)	17.4 ± 0.86 (16–20)	18.0 ± 1.0 (17–19)	18.5 ± 0.5 (18–19)

TABLE 2. CONTINUED.

	Macropholidus ataktolepis, Bosque Cachil (*N* = 9)	*Macropholidus ruthveni,* Bosque Monte Seco (*N* = 24)	*Macropholidus ruthveni,* Coucumayo (*N* = 2)	*Macropholidus ruthveni,* "Chongollapi" (*N* = 2)
SVL (range) (sample size)				
Males	(29.0–35.0) (4)	(31.0–35.5) (5)	34.5	29.0
Females	(38.5–43.0) (3)	(36.0–43.0) (12)	45.5	—
Juveniles	19.5–22.0) (2)	(18.0–24.0) (7)	—	—
Head length/SVL	0.23 ± 0.01 (0.21–0.24) (7)	0.22 ± 0.01 (0.20–0.24) (15)	0.22 ± 0.01 (0.21–0.23)	0.25 (AMNH 38818)
Head depth/head length	0.68 ± 0.06 (0.59–0.79) (7)	0.64 ± 0.03 (0.60–0.72) (15)	0.68 ± 0.0 (0.68)	0.59 (AMNH 38818)
Tail length/total length (complete tails only)	0.69 ± 0.01 (0.68–0.70) (2)	0.68 ± 0.01 (0.67–0.69) (3)	—	—
Body length/SVL	0.50 ± 0.02 (0.48–0.54) (7)	0.51 ± 0.02 (0.48–0.56) (17)	0.54 ± 0.03 (0.51–0.57)	0.47 (AMNH 38818)

*Some data for the "Chongollapi" paratypes of *M. ruthveni* are obtainable only for AMNH 38818 (see text).

178038). Prefrontals hexagonal, in narrow medial contact. Frontal hexagonal, longer than wide, broader anteriorly. Frontoparietals hexagonal with long medial suture, each individually much longer than wide, collectively nearly as wide as long. Interparietal heptagonal, longer than wide. Parietals irregularly polygonal, about as wide as long; equal to or shorter than interparietal. Parietal contacts the upper postorbital on each side (MCZ 178039, 178046, 178050, 178264–67), or parietal and postorbital separated by contact between posterior supraocular and upper anterior temporal (MCZ 178045), or there is narrow parietal–postorbital contact on the right side, which is reduced to a point on the left (MCZ 178038). Three postparietals (occipitals), two lateralmost scales large, hexagonal; medial scale small, pentagonal. First pair of medial dorsal scales on neck (nuchals) distinctly enlarged (broader and wider than following dorsals). Head scales smooth, with scattered pores mostly located around the periphery of dorsal head plates, temporals, and supralabials; a few pits on other head scales.

Lower eyelid with transparent disk. Two subequal supraoculars in direct contact with superciliaries (posterior one in contact with upper postocular; anterior supraocular irregularly hexagonal, posterior one squarish or pentagonal. Four superciliaries (three on one side in MCZ 178039), anterior scale more than twice as large as any other, and overlapping onto top of head. (Noble [1921a: 138] considered there to be five superciliaries in *M. ruthveni,* with the last being the scale here considered the upper postocular. We consider the latter scale part of the postorbital series because essentially none of its area is above the orbit. Noble used neither pre- nor postocular for any of the circumorbital series. Both *ataktolepis* and *ruthveni* typically have only four superciliaries under the present scheme.)

Nostril in extreme posterior part of anterior nasal scale, bulging into anterior part of posterior nasal; anterior nasal larger than posterior nasal (this condition is the same as in *M. ruthveni,* for which Noble [1921a:137] stated the condition as "[n]ostril between the nasals"). Loreal generally large, higher than wide, contacting the posterior nasal, prefrontal, anterior superciliary, preocular, second supralabial, and (except MCZ 178038) also narrowly contacting the frontonasal (see later for exceptions to this pattern).

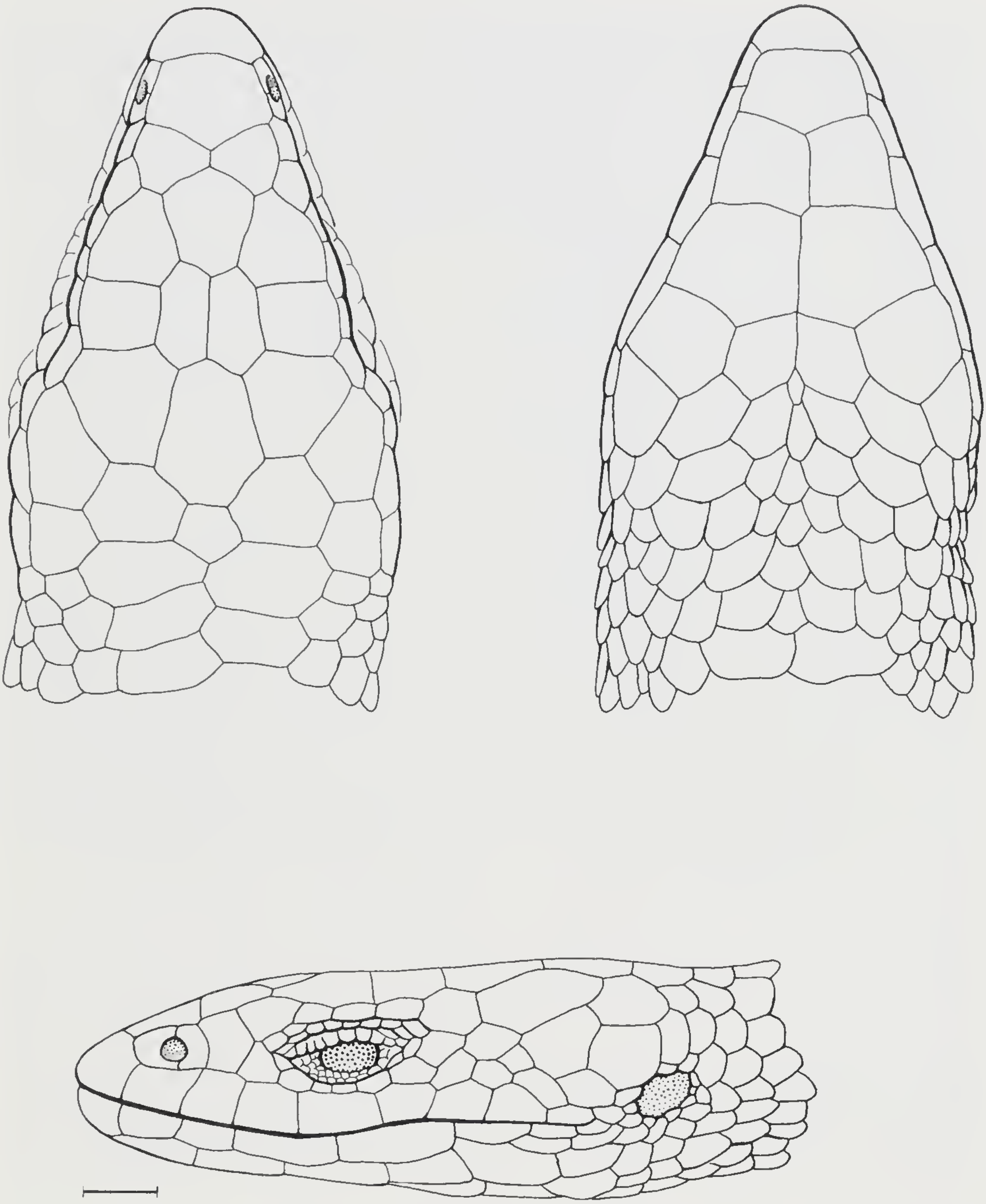

Figure 3. Head of *Macropholidus ataktolepis* in dorsal, ventral, and lateral views (MCZ 178050, female holotype). Bar = 1 mm.

Three unusual loreal conditions were observed: (1) loreal divided transversely into dorsal and ventral portions (MCZ 178039); (2) posterior nasal unusually small and with bilateral dorsal contact between loreal and anterior nasal (MCZ 178266); and (3) bilateral fusion of posterior nasal with ventral portion of loreal, and contact of this enlarged scale with preocular (MCZ 178264); thus, loreal in this specimen does not contact supralabials.

Preocular triangular, small, in contact with loreal, second and third supralabials, and anterior subocular (contact with second supralabial reduced to a point in MCZ 178038 and 178050). Suboculars 3 (MCZ 178045, 178267) or 4 (all others); anterior and posterior scales largest. Postoculars 3, dorsal scale largest, ventral smallest (ventral scale in series with the suboculars, but more than twice as large as any subocular). Supralabials 7 (unilateral conditions of 8 and 6 in MCZ 178039 and 178264, respectively), 4th under eye and also longest.

Temporal region covered by four large polygonal juxtaposed scales (five on one side in MCZ 178046), plus a series (6–11) of smaller polygonal scales located generally anterior and ventral to the enlarged temporals (Fig. 3). Anterior dorsal enlarged temporal contacts upper postocular, parietal, and lateral postparietal (in MCZ 178045 also narrowly contacting posterior supraocular). Posterior dorsal enlarged temporal contacts lateral postparietal and the first transversely enlarged dorsal scale. Posterior ventral enlarged temporal separated from ear by one row of denticles. Ear opening round to vertically oval, bordered by small denticles; tympanum deeply recessed.

Mental with straight posterior margin (Fig. 3). Postmental large, obtusely pointed posteriorly, in lateral contact with infralabials 1–2. Two pairs of genials in contact on midline; anterior pair large, squarish, in contact with infralabials 2–3. Posterior pair large, pentagonal, in contact with infralabials 3–4. Two pairs of enlarged postgenials, anterior pair much larger than posterior pair, separated medially by two (anterior postgenials) to six (posterior postgenials) gular scales; anterior postgenials in contact with infralabials 4 or 4–5; posterior postgenials in contact with infralabials 4 (narrowly) and 5, or 5 only. Infralabials 5 (6 on one side in MCZ 178039 and 178267), 4th longest.

Neck and Body. Anterior gular region (between posterior pair of genials and enlarged gulars; see Fig. 3) filled with small polygonal gular scales in roughly six to seven irregular rows. Posterior gular region (level of posterior margin of ear opening to the gular fold) covered by four to six pairs (5½ pairs in MCZ 178038) of enlarged, rhomboid gular scales, each wider than long. Gular fold weak, ill defined, and without hidden scale rows.

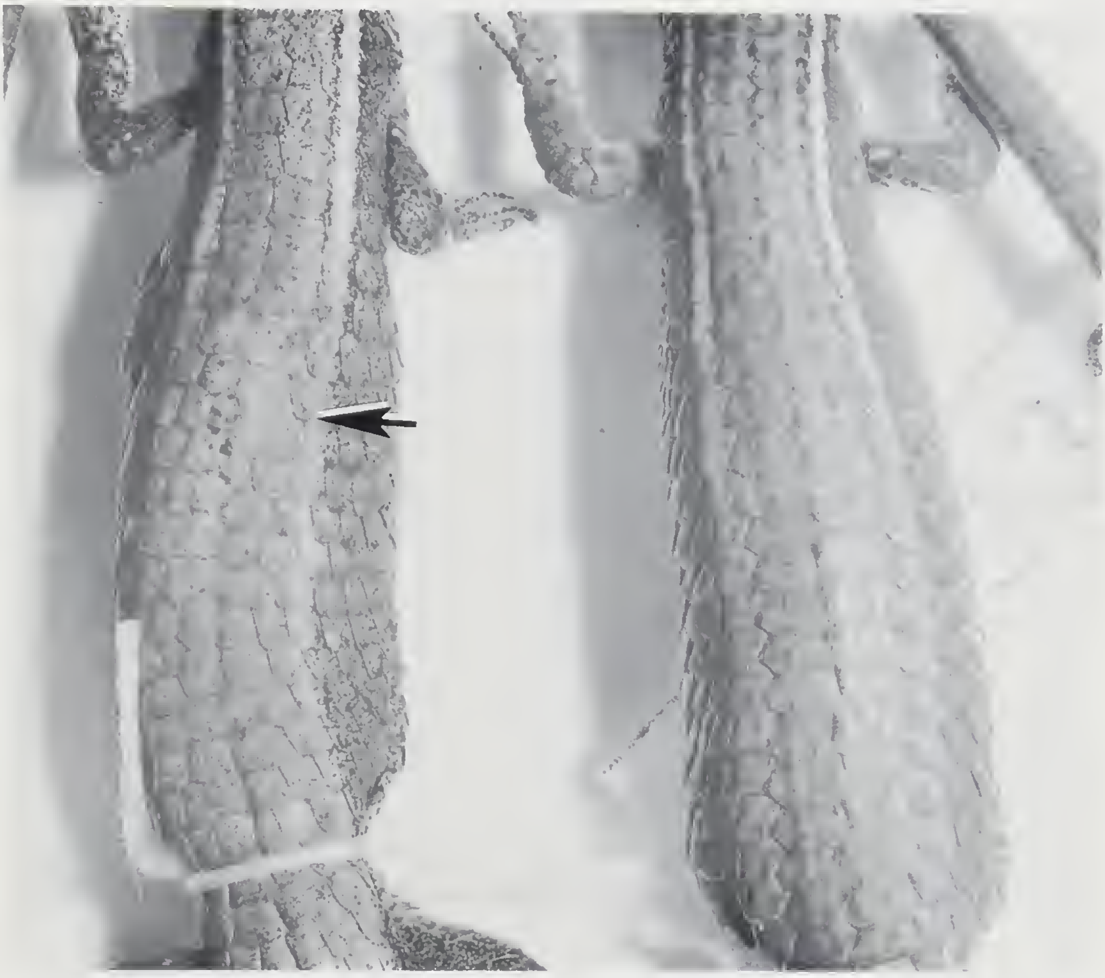

Figure 4. Comparison of dorsal body scalation of *Macropholidus ataktolepis* and *M. ruthveni.* Left: Holotype of *M. ataktolepis* (MCZ 178050), showing the break-up of the enlarged medial dorsals shortly behind the shoulder region (at level indicated by arrow). Right: *M. ruthveni* (ANSP 31765, from Bosque Monte Seco, Rio Zaña, Cajamarca Department), showing array of enlarged medial dorsals continuing to the tail (compare also Fig. 8). Note also the more squarish shape of the enlarged dorsals on the anterior part of the body in *M. ataktolepis* and their more hexagonal form in *M. ruthveni.*

Side of neck anterior to arm covered with medium-sized, rounded, juxtaposed to weakly overlapping scales. Axillary scales small, rounded, juxtaposed.

Dorsal scales of neck in two enlarged smooth rows (medial dorsals); anteriorly each medial dorsal ≥ 2 times as wide as long, gradually becoming more squarish by the shoulder region, continuing in two parallel series, becoming gradually smaller. Medial dorsals bordered on each side by a parallel series of somewhat enlarged paradorsals. Near midbody medial dorsal scales approximately equal in size to lateral body scales, no longer obviously in parallel series (Fig. 4); number of pairs of enlarged medial dorsals varies from 12 to 20: 12 (MCZ 178266), 13 (MCZ 178045), 14 (MCZ 178046, 178265), 15 (holotype, MCZ 178038), 17 (MCZ 178267), 19 (MCZ 178264), and 20 (MCZ 178039). Posterior dorsal scales smooth, squarish, slightly imbricate, in irregular transverse series with lateral body scales (Fig. 4). Usually slight misalignment between lateral and dorsal body scales over middorsal region, caused by differing shapes and slightly different sizes of the two sets of scales. Posterior middorsal scales often irregular in shape (quadrangular to obtusely cycloid) and size. Scales around midbody 18–20.

Lateral body scales smooth, bluntly pointed, imbricate, slightly smaller than posterior dorsal scales. No lateral rows reduced in size, although a few scattered small, imbricate scales about one-half the size of other lateral scales are present. Lateral fold absent.

Ventralmost dorsals (i.e., the scales immediately bordering the ventral plates) somewhat larger than the other dorsal rows. Ventrals smooth, larger than ventralmost dorsals, squarish to rectangular, in four longitudinal rows, in 20–22 transverse rows between limbs. (Noble [1921a] included the ventralmost dorsal rows in his count of six transverse abdominal plates for *M. ruthveni*. Since the scales in these rows have the shape typical of the other dorsals, although slightly larger, they are considered part of the dorsal series here. Both *ataktolepis* and *ruthveni* have four longitudinal rows of *quadrangular* ventrals.) One pair of anal scales; one pair of enlarged preanals. Femoral and preanal pores absent.

Tail and Limbs. Caudal scales at base of tail dorsally and laterally hexagonal, imbricate, weakly striated to very weakly keeled dorsally. Ventral surface of tail with paired series of somewhat enlarged, squarish, smooth, weakly imbricate scales.

Upper surface of arm and hand covered with large, smooth, polygonal, imbricate scales that gradually decrease in size distally. Ventral surface of arm covered with smaller imbricate scales, somewhat conical and nonoverlapping proximally. Anterior, dorsal, and ventral surface of thigh with large, smooth, imbricate, plate-like polygonal scales. Posterior surface of thigh with small conical or pavement-like scales. Lower leg dorsally and ventrally with weakly imbricate scales half the size of those on anterodorsal surface of thigh. Top of foot with large imbricate scales twice or more the size of those on lower leg. Palms and soles covered with small conical to pavement-like juxtaposed scales.

Subdigital lamellae as follows (roman numerals = digits; arabic numbers = range for subdigital lamellae in type series counted on one of each pair of feet for each specimen): forefoot, I 5–7, II 8–10, III 12–14, IV 12–14, V 9; hindfoot, I 6–8, II 9–12, III 13–17, IV 16–19, V 11–12.

Coloration in Life (Holotype). Dorsum medium brown. Top of head grayish brown. Dorsal and ventral surfaces of tail and dorsal surface of hindlimbs dark charcoal gray. Tan dorsolateral stripes from temporal region, fading into dorsal color just behind scapular region; bordered dorsally by dark gray/blackish thin line. Whitish supralabial/neck stripe present. Loreal, temporal, lateral neck regions and flanks dark charcoal gray, paling somewhat on flanks. Anterior gular region dull whitish with grayish wash. Venter similar, but with dull orangish wash in pectoral region and laterally. Edge between belly and flanks and pelvic area speckled with dark blackish flecks. Ventral surface of forelimbs with dull orangish wash and tiny dark flecks.

Coloration in Preservative (Holotype). Top of head and dorsal surface of body grayish brown, becoming greenish gray posteriorly on body, and slate gray on tail. Dorsal head scales and enlarged scales on top of neck heavily and finely speckled with black (speckling on neck concentrated on medial edges of light dorsolateral stripes); the speckling continues onto body but gradually decreases in intensity. Coloration of lateral surface of body and dorsal surface of hindlimbs dark grayish brown, sharply set off from dorsal coloration, heavily speckled with black. Lateral surface of neck and temporal region slate gray, with fine lighter flecks (visible only under microscope). Loreal region and supralabials yellowish brown, heavily suffused with black. Top of forelimbs yellowish brown, heavily speckled with black concentrated proximally. Pale (yellowish) dorsolateral stripe beginning as thin line on anterolateral edge of parietals, widening on enlarged paradorsals of neck (occupying about ⅓ of these scales), gradually fading posterior to shoulder region. Very thin white supralabial stripe beginning at posterior edge of second supralabial, continuing along middle of supralabial row, then dropping to labial border on last two supralabials and continuing to anteroventral border of ear; several scales with light centers forming line behind the ear, but not forming distinct stripe. Ventral surface of head, neck, and body grayish white, finely (on head and neck) to heavily (posteriorly and laterally on body) speckled with black. Ventral surface of forelimbs whitish, with only a few black speckles. Ventral surface of hindlimbs whitish, heavily speckled with black. Palms dusky. Soles dark gray brown. Ventral surface of tail dark slate gray with fine lighter speckling.

The holotype retains more details of coloration and pattern than any paratype, probably as a result of differential preservation. Six paratypes (MCZ 178045–46, 178264–67) are very dark, almost black. The other two (MCZ 178038–39) are essentially as described for the holotype, but the dark ventral pigmentation is more evident, and there is no sharp distinction between the dorsal and lateral body pigment. The dorsolateral stripes are visible in all paratypes.

Comparison of *Macropholidus ataktolepis* with *M. ruthveni*

In general form, body proportions, and coloration, *M. ataktolepis* and *M. ruthveni* are virtually indistinguishable (preserved specimens of both species can differ markedly in color and pattern, but we attribute these differences to the effects of preservation rather than to substantive color differences in life; see the following description of coloration in *ruthveni* for a potential pattern difference between the species). Because scale fusions and some intraspecific variation are characteristic of many species of microteiids generally (the so-called "normal" fusions or divisions that give rise to variation in, for example, the number of supralabial scales), the three scutellational differences between *ruthveni* and *ataktolepis* noted in the diagnosis are commented upon briefly here.

Prefrontal Scales and Other Head Plates (Figs. 3, 5). The presence of paired prefrontal scales between the frontonasal and frontal scale in *ataktolepis* creates differences between *ataktolepis* and *ruthveni* in the shapes of these scales. In *ataktolepis,* both the frontonasal and frontal are hexagonal, with oblique angles posteriorly and anteriorly, respectively. In *ruthveni,* the frontonasal is squarish and the frontal pentagonal, and the two scales meet

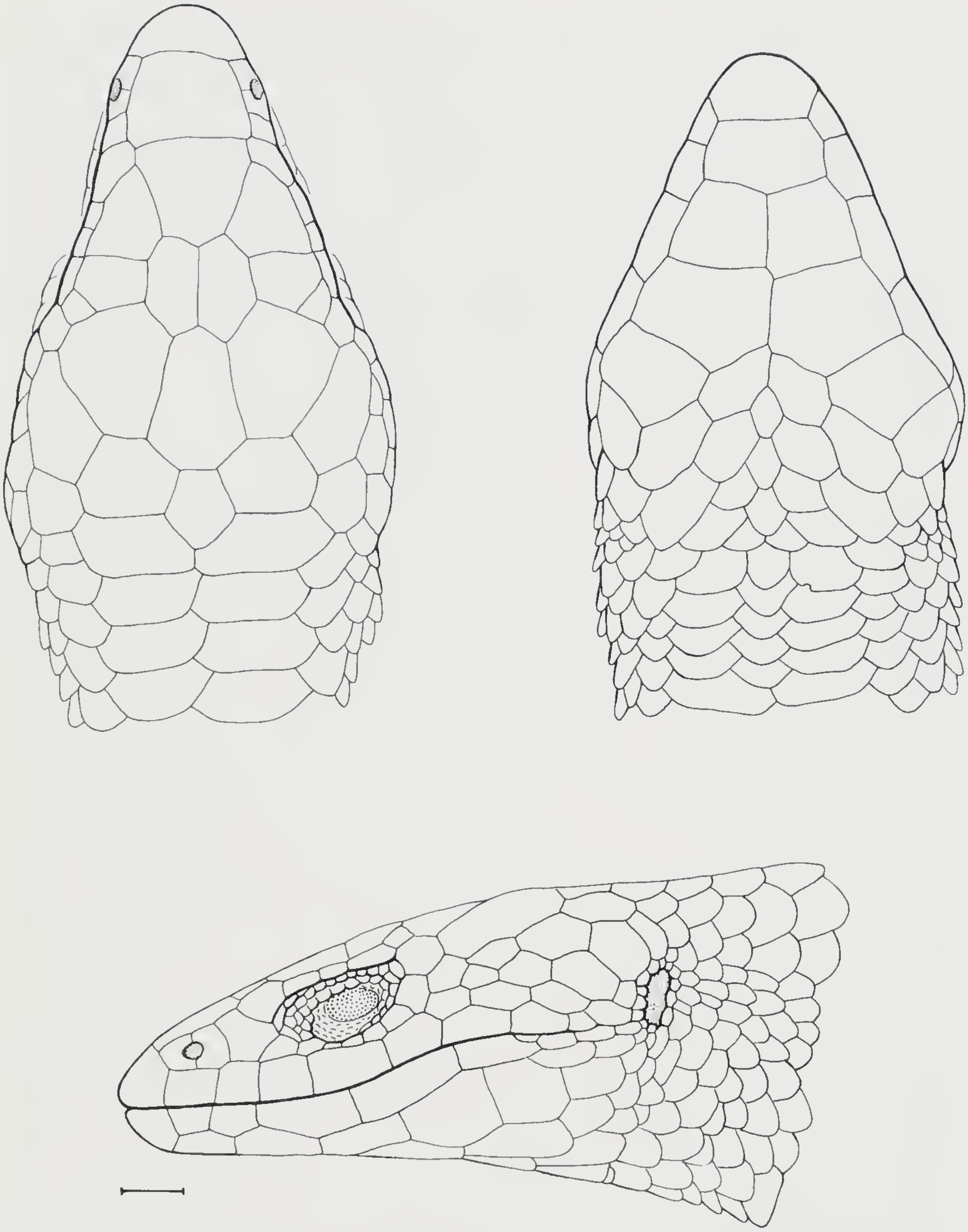

Figure 5. Head of *Macropholidus ruthveni* in dorsal, ventral, and lateral views (MCZ 14041, female holotype). Lateral view is right-side reversed. Bar = 1 mm.

in a straight border. In some individuals of *ruthveni,* the frontal shape might be interpreted as marginally heptagonal, produced by more than point contact between the frontal and first superciliary; in these cases, the frontal still retains a straight anterior border, and the anterolateral sides of the "heptagon" are very short.

The prefrontal scales in *ataktolepis* are well defined and consistent in size, shape, and position in the available specimens (Fig. 3). In the geographically heterogeneous sample of 28 specimens of *ruthveni,* three specimens show significant variation in the region of the frontal/frontonasals. With the exception of MCZ 178036, these cases result in highly irregular and asymmetric scale patterns. MCZ 178036 has a pair of small triangular prefrontals at the lateral juncture of the frontal, frontonasals, and first superciliaries, which appear to have formed from fused portions of each of those scales; they are widely separated on the midline by a broad frontal–frontonasal contact, as is normal in *ruthveni.* The other two *ruthveni* specimens are more aberrant. FMNH 232606 is unusual in the form of the frontal–frontonasal suture on the left side (curved posteriorly rather than straight), and it has two partial sutures within the frontonasal, which partially delimit a large irregular azygous scale on the left side between the frontal and frontonasal. A similar condition is seen in FMNH 232599, except that the supernumerary sutures are complete and the azygous scale itself is longitudinally divided into a medial and smaller lateral portion (the right side of this specimen is, as in FMNH 232606, "normal"). The scales so formed are highly irregular in shape and do not approach the regular prefrontal shapes seen in all specimens of *ataktolepis.*

The only unusual conditions of head plates in the series of *ataktolepis* are (1) the nearly complete fusion of the left frontoparietal with the posterior supraocular in MCZ 178045, a fusion also seen in a paratype of *ruthveni* (MCZ 147313; Noble [1921a: 139] stated that this was on the left side of one of the paratypes, but it is on the right side of MCZ 147313 and none of the other paratypes has this condition); and (2) the fusion of each posterior nasal scale with the corresponding ventral portion of the loreal (MCZ 178264), as already described.

Prefrontal scales vary in their presence/absence within and among species of the presumably (see later) closely related genus *Pholidobolus.* Other than *Pholidobolus macbrydei,* however, in which the condition is apparently variable (Montanucci, 1973: 16), prefrontals are typically present or absent in the other species.

Montanucci (1973:37) stated that there was a "high frequency" of prefrontal scales in *P. macbrydei* but did not give a specific proportion, nor state whether the variation was intra- or interpopulational; in a sample of six *macbrydei* from widely separated geographic areas (Cotopaxi and Azuay Provinces, Ecuador; MCZ 154631–33, 163958–59), all individuals lacked prefrontals. It is the characteristic shape and population-specific nature of the prefrontals in *Macropholidus ataktolepis,* their absence in a geographically heterogeneous sample of *ruthveni,* and the coincidence of this character with unusual dorsal scale pattern (described in greater detail later) that lead us to interpret the nature of the prefrontals as characteristic of *M. ataktolepis.*

A high proportion of scale aberrancies in *ruthveni* involving the region of frontal–frontoparietal contact is perhaps significant, in that this region gives rise to one of the diagnostic differences between *M. ruthveni* and *M. ataktolepis.* Such an association between intraspecific variants and interspecific differences has been inferred for interspecific scale differences in one other group of microteiid lizards (Donnelly *et al.,* 1992).

Dorsal Scales of the Body (Fig. 4). The paired series of vertebral scales in both *Macropholidus ruthveni* and *M. ataktolepis* begin on the neck as transversely elongate hexagonal or rectangular scales. In both species (but seemingly more so in *ataktolepis* than in *ruthveni*; see Fig. 4), they become gradually more squarish posteriorly by extension in the longitudinal dimension, usually noticeably so just behind the shoulder region. In *ruthveni,* the enlarged scales continue virtually to the tail base (Figs. 4, 8). In *ataktolepis,* however, there is a generally rather abrupt transition to small dorsals by midbody (Fig. 4). The posterior dorsal scales behind this transition zone in *ataktolepis* are slightly larger than the lateral body scales at the same level and usually have straight posterior borders, in contrast to the bluntly pointed borders of the lateral scales. The transition to smaller scales in *ataktolepis* is sometimes accompanied by slight irregularities in the arrangement of dorsal scales, caused by varying scale sizes in the transition zone.

A comparison of the number of pairs of enlarged vertebral scales relative to the total number of transverse rows of dorsal scales (occiput to posterior margin of the leg) demonstrates this differ-

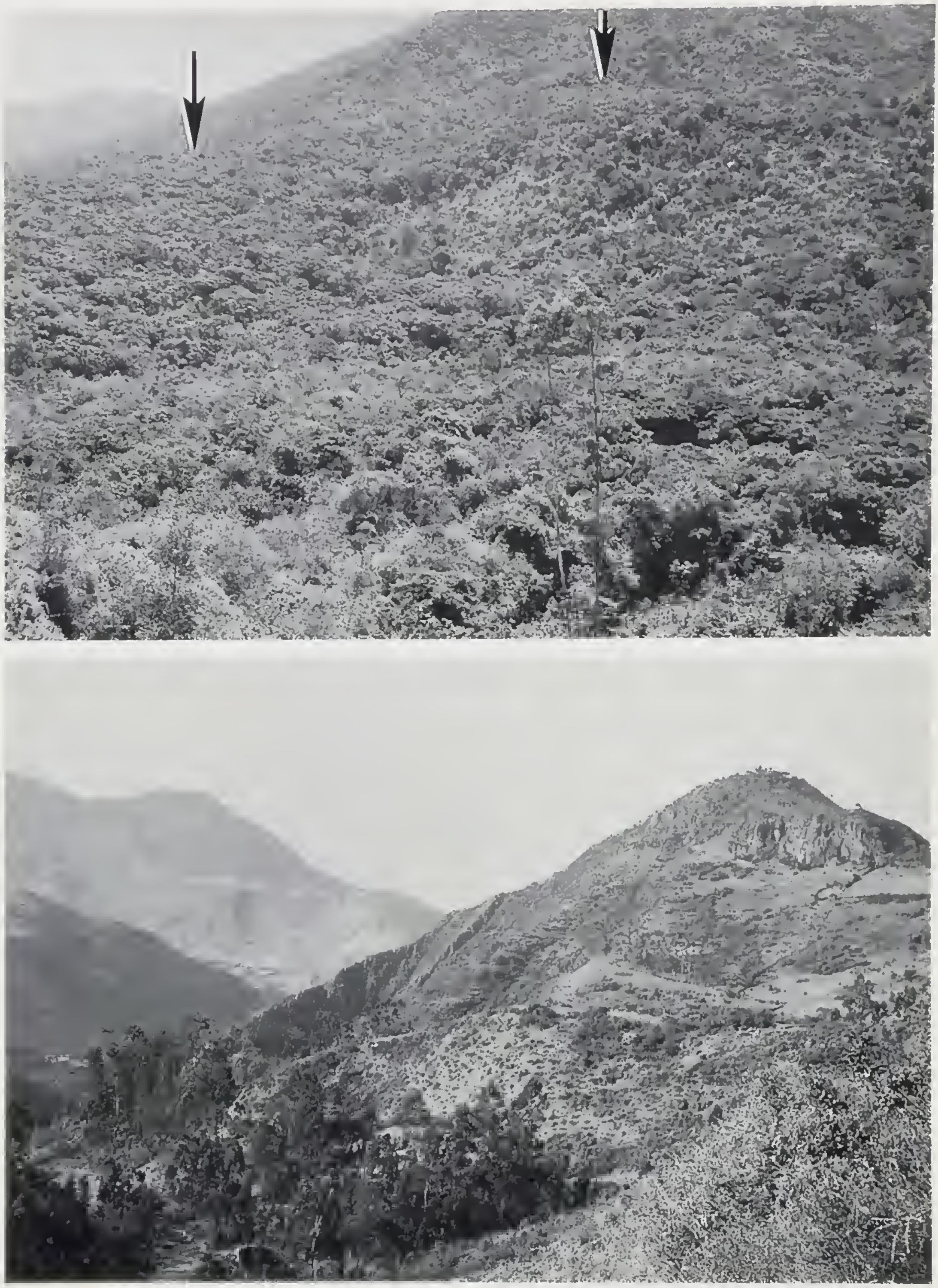

Figure 6. Top: Bosque Cachil as seen from the slope on the opposite side of the valley. Arrows mark the approximate upper extent of forest, above which is short bushy vegetation. The forest extends to the left and right off both sides of the photograph, but most of its extent is encompassed within the photograph. Bottom: General view of the terrain immediately down the valley from Bosque Cachil. Most slopes are denuded of vegetation. The trees in the lower left are *Eucalyptus*. Both photographs were taken on 28 September 1991.

ence between *ruthveni* and *ataktolepis* well. Both species have comparable total numbers of scales in this area (32–37 in *ruthveni*; 29–35 in *ataktolepis*), but the number of pairs of enlarged dorsals in *ruthveni* is 25–34 (average of 3.3 for the difference between total transverse dorsals and enlarged dorsals), whereas in *ataktolepis* it is only 12–20 (average of 17.4 scales difference) (see Table 2).

Temporal Scales (Figs. 3, 5). All specimens of *M. ataktolepis* have a regular arrangement of four enlarged temporal scales (Fig. 3; MCZ 178046 has five on one side), and the total number of temporal scales (the region bounded by the postoculars, supralabials, parietals–postparietals, and the anterior margin of the ear) is 10–14 on each side. On the other hand, the arrangement of temporal scales in *ruthveni* is more irregular (Fig. 5). The fragmentation of scales in the temporal region in *ruthveni* makes the delineation of "enlarged" from "normal" temporals a somewhat arbitrary distinction, as there is often a continuous gradation in scale sizes. The total number of temporal scales in *ruthveni* is 11–21, with the number that might be considered "enlarged" ranging from 1 to 7 (mode = 4, with other strong modes at 2 and 5). Some individuals of *ruthveni* are highly asymmetrical in the number and size of temporals on each side; this was not observed in any *ataktolepis.*

Distribution, Habitat, and Natural History

Macropholidus ataktolepis is known only from the type locality, "Bosque Cachil." The following observations are largely extracted from Cadle's field notes made during a visit to Bosque Cachil on 28 September 1991 (see Figs. 6, 7). The site presently has a small remnant of humid forest lying in a montane valley (Fig. 6), at the bottom of which is a small stream, known locally as Quebrada Cachil. Most of the forest is between 2,400 and 2,500 m, with some riparian forest extending somewhat lower. Dillon *et al.* (1994) estimated the area of Bosque Cachil at about 100 ha. Surrounding the forest, the general habitat is scrubby chaparral-like bushland and disturbed terrain and obviously much drier (Fig. 6); however, the original extent of forest prior to human intervention is unknown and possibly was not much greater than at present. Montane forests this far south in the western Andes of Peru are usually

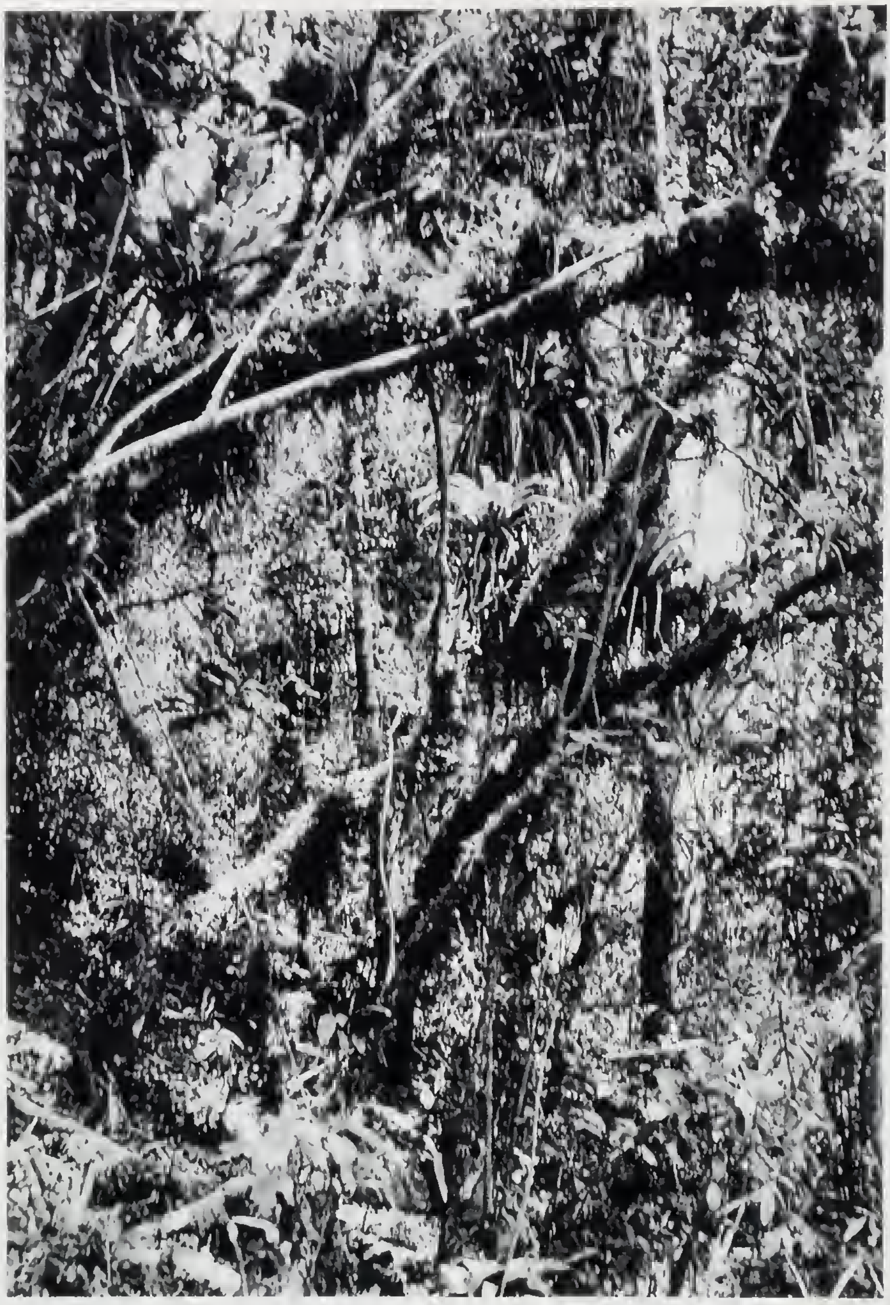

Figure 7. Understory vegetation at Bosque Cachil, showing generally small, short-statured trees, but with abundant mosses and, in this view, bromeliads. A relatively long exposure due to low ambient light level resulted in slight fuzziness in the photograph. Photographed 28 September 1991.

quite localized because local features of climate and aspect limit the extent of forest development (see H. W. Koepcke, 1957, 1961; H. W. Koepcke and M. Koepcke, 1958).

The end of September, when these observations were made, is well into the dry season (approximately May to December in this portion of the Andes in Peru). At that time, the general aspect of Bosque Cachil was quite dry, although clear evidence of seasonal humidity was present. The forest is dominated by *Podocarpus,* with lesser amounts of *Clusia* and *Guarea.* Some large bromeliads were present (Fig. 7), but nowhere were these dense. Orchids were present but not abundant, but no tree ferns (*Cyathea*) were seen. Mosses festooned most trees, but at this time these were all dry, crackly, and brown. Another indication of the dryness was the fact that soil under even large boulders was dry. The lower part of the valley below Bosque Cachil is scrubby chaparral-like bushland and secondary growth, including introduced *Eucalyptus* (Fig. 6). According to local inhabitants, the area is quite wet and cold from about January to April, sometimes with dense fog. The characteristics of the streambed at the bottom of the valley give another indication of the seasonal abundance of water at Bosque Cachil. In September 1991, stream flow was reduced to approximately 1–2 m wide at most points. However, the channel is deep and scoured in places, with many moss-covered boulders, cascades, and deep pools. This suggests much greater water flow during parts of the year. During a visit to Cachil on 17 May 1993, M. O. Dillon (personal communication) reported a constant rain of about 2 hr, with high humidity lasting through the afternoon and evening.

The forest of Cachil was apparently not studied by Hans and Maria Koepcke during their extensive surveys of the western Andean forest remnants of Peru (H. W. Koepcke and M. Koepcke, 1958; H. W. Koepcke, 1957, 1961; M. Koepcke, 1954, 1961). They did, however, study several other forest isolates on the south side of the Rio Chicama valley. They characterized the forests of Hacienda Llaguen (07°40′S, 78°40′W), directly south of Bosque Cachil across the Rio Chicama valley, and spanning comparable elevations (1,700–2,900 m), as "[c]actus and bushsteppe; transition to riparian forest and mesothermic rainforest; light evergreen mountain forest to primary rainforest of the oligothermic zone in some places . . . between 2400 and 2900 meters" (H. W. Koepcke, 1961:31). The forest of Cachil, in both elevational zone and dominant vegetation, appears to correspond well to the "oligothermic rainforest zone," characterized by the presence of *Podocarpus* and trees locally densely covered with epiphytes (H. W. Koepcke, 1961:164).

In general respects, the climatic regime (rainy season roughly January to April) appears similar to that at another forest isolate just north of Bosque Cachil, Bosque Monte Seco on the Rio Zaña (see Cadle, 1989, 1991; Cadle and McDiarmid, 1990; Sagástegui and Dillon, 1991). However, despite the presence of abundant mosses on the trees and a similar floral composition, Bosque Cachil has a drier aspect and is at a slightly higher elevation (2,400–2,500 m) than much of the humid forest at Monte Seco (1,500–2,500 m). Indicators of the greater aridity at Cachil include fewer streams, and those present with reduced water flow; shorter-stature forest in general; reports by locals of only occasional dense fog during the rainy season (ubiquitous during the rainy season at Bosque Monte Seco); and the absence of tree ferns (although possibly these were removed by earlier inhabitants of the region, as they are used medicinally; tree ferns, however, are common at Bosque Monte Seco; see Sagástegui and Dillon, 1991; Dillon *et al.,* 1994).

The flora of Bosque Cachil appears to be a small subset of that at Bosque Monte Seco (Sagástegui and Dillon, 1991; M. O. Dillon, personal communication), although with different dominant elements. Whereas the forest of Cachil appears to correspond to Koepcke's (1961) "oligothermic" rainforest, the more humid forest of Bosque Monte Seco corresponds more with the "mesothermic rainforest" and "cloud forest" habitats discussed by Koepcke (1961), which in general occur at slightly lower elevations in western Peru than the "oligothermic rainforests" (H. W. Koepcke, 1961). Other than an enigmatic species of *Dipsas* (Colubridae), no species of amphibians or reptiles presently known from Bosque Cachil occur also at Bosque Monte Seco, but much more extensive sampling of the herpetofauna needs to be done at Cachil.

All specimens of *Macropholidus ataktolepis* were collected under rocks during the day. This species is presumably diurnal, as is its close relative *M. ruthveni* (see later). One female (MCZ 178045) collected on 17 May contained one developing follicle, whereas the female holotype, collected at the end of September, and MCZ 178264, collected in December, contain no yolking follicles. The only other amphibians or reptiles now known from Bosque Cachil are undescribed species of *Stenocercus* (Tropiduridae), *Dipsas* (Colubridae), and *Eleutherodactylus* (Leptodactylidae) presently under study and a species of *Gastrotheca* (Hylidae).

NOTES ON *MACROPHOLIDUS RUTHVENI* NOBLE

Types, Type Locality, and a New Series from the Rio Zaña

Noble (1921a:138) described *Macropholidus ruthveni* on the basis of four specimens: the holotype and one paratype in MCZ and two additional paratypes in AMNH. The holotype, MCZ 14041 (Figs. 5, 8), is from "Coucumayo, a half-way station between the towns of Huancabamba and Tabaconas" (Noble (1921a: 139), and MCZ 147313 (originally MCZ 14043) is from "Chongollapi" (=Chongoyape; see additional comments on localities later). The two AMNH paratypes, AMNH 38817–18, were both originally cataloged with "Coucumayo" as the locality. However, Noble (1921a:139) stated that two specimens were obtained at each of the two localities mentioned in the type description; hence, one of the AMNH specimens is from Coucumayo and the other from Chongoyape. Noble gave sufficient detail in his description to identify AMNH 38818 as the "Chongollapi" specimen (21 ventral scales between the collar [=gular fold] and the anal plates, and presence of a third supraocular in one of the Chongoyape specimens, as is the case in the holotype; AMNH 38818 is the only paratype that satisfies these criteria). AMNH 38817, then, is the other specimen from the type locality, Coucumayo.

We have not found Coucumayo (stated by Noble to consist of a single house) listed in gazetteers or on maps, but Noble's description places it on the eastern spur of the Cordillera Huancabamba on the border between the departments of Piura and Cajamarca (Fig. 2). According to Noble (1921a:139), Coucumayo is "one of the highest points of the trail but is probably not over 8,000 feet [=2,440 m] in altitude." Most parts of the cordillera between Huancabamba and Tabaconas rise well over 3,000 m, but a break with maximum elevations between 2,000 and 3,000 m occurs 18–20 km southeast of Huancabamba at approximately 05°20′S, 79°20′W (1:480,000 maps for the departments of Piura and Cajamarca, Instituto Geográfico Nacional, Lima). This is the present location of the main route between Huancabamba and Tabaconas. Based on the elevation stated in the description, the type locality of *ruthveni* is most likely along this part of the ridge. Thus, the type locality is east of the continental divide in upper reaches of the Rio Huancabamba/Chamaya drainage.

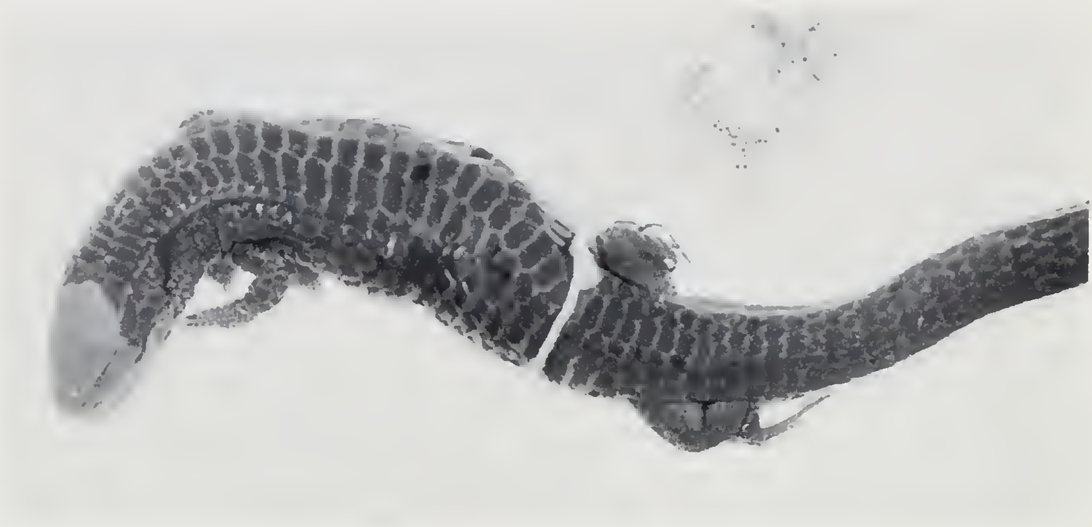

Figure 8. Holotype of *Macropholidus ruthveni,* MCZ 14041, an adult female. Noble (1921a:139) stated that the light borders of the scales visible in the type were "not so distinct" in life. He also did not mention the dorsolateral stripe, visible faintly in the photograph.

Noble did not give information about the general environment of Coucumayo, stating only that the two specimens of *Macropholidus* collected there were from a pasture. Huancabamba lies in a dry rain-shadow valley (Noble, 1921b; T. A. Parker *et al.,* 1985); however, humid forest persisted even recently at elevations above 2,100 m on the slopes north and east of Huancabamba (T. A. Parker *et al.,* 1985) and possibly lower in 1916 when Noble

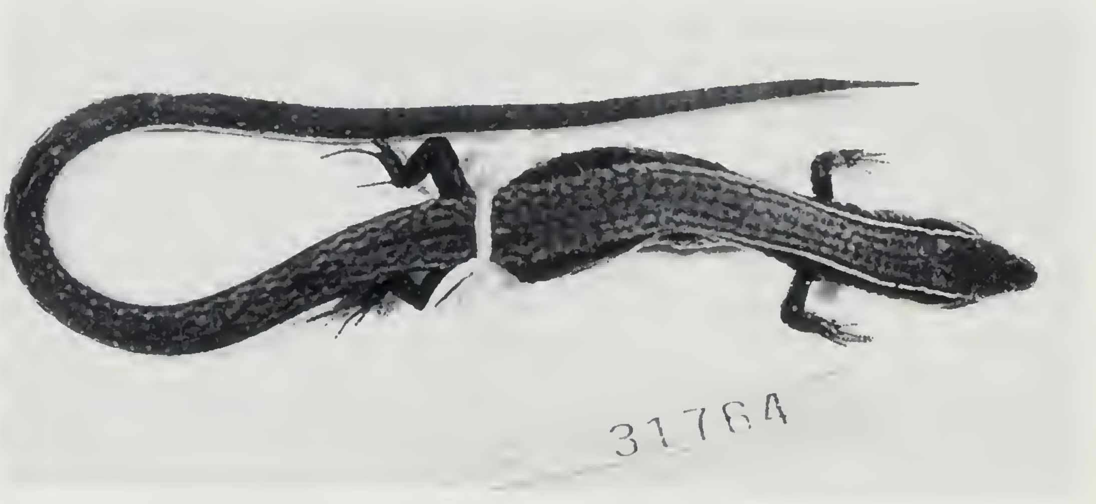

Figure 9. Dorsal view of *Macropholidus ruthveni* (ANSP 31764), an adult female from Bosque Monte Seco, Rio Zaña valley, Cajamarca Department, Peru.

visited the area. Tabaconas itself lies in a valley characterized by humid montane forest (Barbour and Noble, 1920; T. A. Parker *et al.,* 1985).

Noble purchased two of the paratypes (MCZ 147313, AMNH 38818) in Chongollapi (=Chongoyape) from a restaurant keeper, who had preserved them in aguardiente. Chongoyape is at 200 m elevation on the Rio Reque in the coastal desert region, Lambayeque Department, 06°39′S, 79°24′W (Fig. 2), but Noble suggested that the specimens probably came from "some of the high altitudes fifty or a hundred miles inland." This assessment makes sense with respect to natural history observations for *ruthveni* made by Cadle on a population at the Rio Zaña (see later). It seems unlikely, therefore, that *ruthveni* would be found in low coastal desert (but see discussion of KU 220845, later). Noble's estimate, however, of "fifty or a hundred miles inland" is probably a substantial overestimate, whether considered in airline or trail distances; the nearest humid forests are about 50 km airline distance and 100 km by the existing road east of Chongoyape (Cadle, personal observations).

Presently, the type specimens of *M. ruthveni* are in fair condition and somewhat soft (the MCZ paratype is a small juvenile, which has had its head removed, critical–point–dried, and mounted for scanning electron microscopy; the mounted head still retains the outline of the head scutellation). The holotype (Fig. 8) is an adult female, AMNH 38817 is an adult male, and AMNH 38818 is probably a male based on swelling of the tail base.

In addition to the type series, we studied a series of *ruthveni* collected by Cadle from the upper Rio Zaña (Bosque Monte Seco), Cajamarca Department (Figs. 2, 9; for details concerning the area, see Cadle, 1989, 1991; Cadle and McDiarmid, 1990; Sagástegui and Dillon, 1991). These specimens include ANSP 31764–69; FMNH 231771, 232599–608; MCZ 178036–37; and JEC 7202, 7211, 7463, 7528, 7798–99, 8062. All of these specimens are from within a 3-km airline radius north to east of Hacienda Monte Seco, Rio Zaña, Cajamarca Department, Peru (79°07′W, 06°51′S; Fig. 2). KU 220845, which we refer provisionally to *M. ruthveni,* is from Chaclacayo, Lima Department, a locality far south of the other known localities for *ruthveni* (Fig. 2). Details concerning this specimen are given later, but it was not included in the summaries of variation for *ruthveni* immediately following. Data on the type series and the Rio Zaña sample of *Macropholidus ruthveni* are summarized here, as are observations on the natural history of this species at the Rio Zaña study site.

Descriptive and Variational Comments

The series referred to *Macropholidus ruthveni* from the Rio Zaña (Bosque Monte Seco; see Fig. 9) is similar to the type series in all scutellational features, except for what might be considered normal (and, in this case, minor) intraspecific variation. Table 1 gives measurements and scale counts of the holotype of *M. ruthveni,* and Table 2 summarizes scutellation and mensural features in all samples of the species. The following comments augment the characterization given by Noble (1921a).

Noble (1921a) noted several minor variations in head scalation in the type series, and the larger series examined by us does not significantly alter his characterization. Some of the variation was already discussed in the context of comparing *ruthveni* and *ataktolepis.* Other variations are noted here. Virtually all specimens have two large supraocular scales on each side. The holotype differs in having three supraoculars on each side, the third being a small quadrangular scale formed by a short suture across the posterolateral portion of the second supraocular (Fig. 5). One other specimen, AMNH 38818 from Chongoyape, has three supraoculars on the right side, similar to the pattern in the holotype, and the usual condition of two supraoculars on the left side. No specimens from the Rio Zaña showed this variation.

Proportional measurements and meristic counts for the specimens of *ruthveni* we examined are as follows. Complete tail 2.03–2.26 times SVL in three adults, 1.61–1.87 times SVL in five juveniles, and 0.62–0.69 times TL (adults and juveniles combined). The holotype, a female (SVL 45.5 mm), is the largest specimen. Range of SVL for other females was 36–43 mm, greater than the range for males (29–35.5 mm). The forelimb extended forward reaches the posterior border or middle of the eye.

Superciliaries usually four, occasionally three or five (Noble included the scale we consider the upper postocular in his superciliary series, and therefore stated the condition in the type series as five superciliaries); postoculars usually three, occasionally two.

Supralabials seven, with the fourth under the midpoint of the eye (eight and six on two sides each). Infralabials five (six on one side, four on two sides). Scales around the middle of the body 17–20 (19.3 ± 0.73). A distinct loreal, higher than wide, separating the posterior nasal from the preoculars.

No lateral body fold or lateral scales of reduced size. Four transverse rows of quadrangular ventrals (Noble's count of six rows included the ventralmost rows of dorsals; see the comments in the comparison of *ataktolepis* with *ruthveni*).

Subdigital lamellae as follows (roman numerals = digits; arabic numbers = range for subdigital lamellae counted on one of each pair of feet for each specimen): forefoot, I 5–7, II 8–11, III 11–14, IV 11–16, V 7–9; hindfoot, I 6–8, II 10–12, III 12–15, IV 16–20, V 10–12.

Distribution

The new series of *Macropholidus ruthveni* from the Rio Zaña is from about 175 km south of the type locality and in the southerly adjacent river valley to the Rio Reque system, from which the two "Chongollapi" paratypes presumably came (Fig. 2). Other species of amphibians and reptiles known from the Rio Zaña study site, including *Stenocercus percultus, S. eunetopsis, Telmatobius latirostris,* and *Philodryas simonsi* (Cadle, 1991, and personal observations), are also known from montane forests of the upper Rio Reque. To the extent that the distribution of *M. ruthveni* is representative of the same pattern, Noble's suspicion that the two "Chongollapi" paratypes of *ruthveni* were from higher elevations east of Chongoyape seems likely. This species thus appears to be another example of a taxon occurring in humid montane forest isolates on the western slope of the Andes in northern Peru and might be expected in other similar forests of this area (see Cadle, 1991:85–89, for discussion and other examples). As is the case for *Telmatobius latirostris* and several other elements of the west slope herpetofauna of northern Peru (Cadle, unpublished data for the Bosque Monte Seco herpetofauna), *Macropholidus ruthveni* also occurs east of the continental divide (the type locality is in the upper Rio Huancabamba drainage; Fig. 2).

If the population represented by KU 220845 proves to be referable to *Macropholidus ruthveni* (see discussion later), then it is widely disjunct from the nearest known more northern locality (Fig. 2). Moreover, this would imply that the range of *ruthveni* encompasses that of *ataktolepis.* However, given the fragmented nature of habitats for *ruthveni* in northwestern Peru, any areas of sympatry are likely to be quite narrow or restricted to single forest isolates (see Montanucci, 1973:20–24, for a similar pattern for montane *Pholidobolus* in Ecuador).

At the Rio Zaña study site, *Macropholidus ruthveni* was collected between 1,440 and 2,210 m elevation. The only other elevational data for the species is Noble's statement (1921a:139) that the type locality was "probably not over 8000 feet [=2,440 m]."

Coloration in Life and Preservative

The following color notes are based on a detailed field description of FMNH 232602 (female), with supplemental notes from 35-mm Kodachrome transparencies. The coloration is nearly identical to that already described for *M. ataktolepis.* Dorsum medium brown with fine black specks, becoming grayish brown toward head, grayish on tail. Lateral surface of body darker brown to grayish, more or less abruptly set off from dorsal coloration; becoming darker on neck and temporal region. Dorsolateral golden stripe begins behind eye and fades rather abruptly at approximately midbody (see Fig. 9). Cream-colored labial stripe begins on upper labials and extends to base of forearm. Tail dark gray with obscure small dark spots dorsally. Chin white. Belly yellowish white, golden toward sides. Ventral surface of tail gray with darker markings.

The coloration of *Macropholidus ruthveni* in preservative is essentially like that of *M. ataktolepis.* The amount of dark ventral pigment varies enormously, from almost none to essentially the entire venter very dark, in the series available. The chin and throat, however, are usually paler than the rest of the venter. The dorsolateral stripe in *ruthveni* occasionally (e.g., ANSP 31764, FMNH 232605) continues as a vague discontinuous line extending anteriorly along the superciliary scales and canthal region. Both *ruthveni* and *ataktolepis* have a supralabial stripe extending to the anterior margin of the ear. In the Rio Zaña specimens of *ruthveni,* this stripe continues posterior to the ear for some distance, and in most specimens extends to the base of the forelimb. In the small series of *ataktolepis,* at most only a few scales posterior to the ear have whitish pigment, resulting in a line of small white dots; in no case do these form a continuous line or extend farther than the midpoint between the posterior margin of the ear and the base of the forelimb. This pattern difference may prove to be a consistent difference between the two species, although we hesitate to conclude this given the small samples presently available for *ataktolepis* and differences in preservation between the *ruthveni* and *ataktolepis* samples.

Noble (1921a) did not describe the colors in life of the types of *M. ruthveni* in any detail, noting only that the ground color was "browner" than the blackish coloration in preservative (see Fig. 8). Curiously, he mentioned neither the dorsolateral light stripes nor the light supralabial-ear stripe characteristic of the Rio Zaña population of *ruthveni.* The state of preservation of the type series is such that details of pattern are difficult to discern. However, the dorsolateral light stripes are clearly visible in all specimens of the series (see Fig. 8); they extend from the supraoculars and fade on the body behind the shoulder. The supralabial-ear stripe is less discernible. It is visible in the holotype as a vague light line below the eye; the posterior and anterior extent cannot be discerned. In AMNH 38817 it is visible as a broken line extending from below the eye to the anterior margin of the ear.

Habitats and Activity

Habitats in which *Macropholidus ruthveni* occurred at the Rio Zaña study site spanned a range: relatively pristine montane cloud forest, secondary and disturbed forests, overgrown to relatively open cafetals, and open brushy hillsides. All active specimens were encountered during the day from midmorning (0945 hours) to late afternoon (1700 hours), usually in areas with much leaf litter (although they were also found crossing open trails or dirt roads). Many specimens also were found inactive during the day under rocks (occasionally logs) or, in one instance, under moss 1.5 m above the ground on a large boulder. Noble (1921a:139) stated that two specimens of the type series were collected under flat rocks in a pasture. One specimen from the Rio Zaña (FMNH

232605) was disgorged by a specimen of the colubrid snake, *Coniophanes longinquus* (Cadle, 1989).

Reproduction and Communal Nesting

Females of *Macropholidus ruthveni* with eggs were collected at the Rio Zaña study site on 15–18 January and 17 June; in addition, egg clutches were discovered on 17 June (see the following). Five females (FMNH 232603, 232608, collected in June; ANSP 31764, 31767, 31769, collected in January) contained two eggs each; ANSP 31765, collected in January, contained one. Hatchlings (FMNH 232599–600, JEC 7528; SVL 18–19.5 mm) were collected on 14 May and 18 June. These observations span the early rainy season (January) and early middle dry season (May to June), and suggest either a lengthy or multimodal period of reproduction in this population.

Communal nesting is known in a variety of lizards and snakes and is probably more widespread than has been reported. The only published records for teiids are for the macroteiid *Kentropyx calcaratus* (Magnusson and Lima, 1984) and the microteiid *Neusticurus ecpleopus* (Uzzell, 1966). In addition to observations reported here for *Macropholidus ruthveni,* Cadle has observed one instance of communal nesting in another microteiid, *Proctoporus bolivianus,* in southern Peru (Upper Rio Santa Maria, Cuzco Department). The communal nesting habits of *Macropholidus ruthveni* were observed at Bosque Monte Seco in the Rio Zaña valley, Cajamarca Department, Peru (for discussion of this locality, see Cadle, 1989, 1991; Cadle and McDiarmid, 1990). In this case, the communal nest of *M. ruthveni* was coincident with a communal nest of the colubrid snake *Dipsas oreas.*[4]

These observations were made by Cadle on 17 June 1987 at 1,490 m elevation at the Rio Zaña study site. On that date, he observed a *Macropholidus ruthveni* crossing a dirt road and seeking refuge in a hole close to the base of the adjacent road embankment, which was a mixture of clay and small rocks. Upon digging to extract the lizard, a communal nest of this species was discovered, and with little further digging several snake eggs and egg shells were discovered. The eggs were laid in a crevice (1–3 cm wide and 15–20 cm in vertical dimension) beneath a loose conglomerate of flaky rocks and clay. The crevice was lined mostly with moist clay mixed with some gravel. Lizard eggs were found between 5 and 30 cm from the entrance to the crevice. The snake eggs were found between 20 and 30 cm from the entrance and were intermingled with the lizard eggs. Although eggs were found up to 30 cm from the opening, since the crevice was oriented roughly parallel to the face of the roadcut, the deepest part of the crevice was only about 15 cm from the surface of the soil. Because the road embankment faced roughly eastward and was not covered or overshadowed by dense vegetation, the soil at this site probably would have been warmed daily by the morning sun.

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[4] This species has been taxonomically confused (see Orcés and Almendáriz, 1987; Kofron, 1982) and has not been previously reported from Peru. Specimens recently collected by Cadle at several localities in northern Peru, and additional museum specimens to be reported elsewhere, are tentatively identified as *Dipsas oreas* pending further study of geographic variation in this complex. These collections confirm the species' presence in humid montane forests of the western Andes of Peru south to at least the Rio Zaña.

Both the microteiid and the snake eggs were apparently of varying ages (minimally, two viable snake clutches were present, plus one recently hatched clutch). The remains included some microteiid eggs that were already well decomposed, other more recent shell remains, and several unhatched eggs. A total of 220 microteiid shell remains were found (this is a minimum count), plus eight viable eggs, one of which hatched the next day (FMNH 232599; SVL 18 mm). The first snake eggs encountered included five empty shells together in a group; a bit farther in were three additional shells that looked roughly the same age as the first five and might have been part of the same clutch. A second clutch included seven viable eggs. The deepest clutch included five viable eggs plus one fungus-ridden egg. These two latter clutches had embryos of slightly different ages when one egg of each was opened on 18 June (the deepest clutch had a smaller embryo).[5] Clearly the microteiid nest represents a true "communal" nest, with many females contributing eggs. The same is probably true for the snake clutches, although improbably they could represent successive clutches of a single female.

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[5] Five of the snake eggs were transported to Lima on 27 June, where they were kept in moist paper towels in a plastic bag while fieldwork was completed elsewhere in Peru. They were then transported back to the United States, where they hatched between 23 September and 1 October. Egg-laying in subterranean retreats may seem an unusual behavior for "arboreal" snakes such as *Dipsas oreas.* Although

Notes on KU 220845, Tentatively Referred to *Macropholidus ruthveni*

KU 220845 was collected at Chaclacayo, Lima Department, Peru, 11°59′S, 76°46′W, by M. Urbina, date unknown. This locality is approximately 620 km south of the nearest known locality for *M. ruthveni* (Rio Zaña valley; see Fig. 2), but a series of specimens from Chaclacayo is apparently now available and will be reported on elsewhere by Antonio W. Salas and his colleagues (personal communication). Measurements of the KU specimen are as follows: SVL 31 mm, HL 7.21 mm, HW 4.5 mm, HD 3.25 mm, BL 15.9 mm, and TL 38 + 2 mm. Meristic counts (e.g., Table 2), the arrangement of head plates and body scales, and aspects of pattern of KU 220845 are within the range of those already reported for the types and Rio Zaña samples of *M. ruthveni.* However, the specimen is unusual in the following features: (1) the loreal scale is completely fused with the posterior nasal scale on both sides in KU 220845, whereas in all other specimens of *ruthveni* examined, the loreal is present as a discrete scale; and (2) the paired series of enlarged medial dorsal scales are incomplete and irregular on the posterior part of the body. There is a suggestion that scales of the temporal region in KU 220845 are broken up more than in the other specimens of *ruthveni,* but this difference is subtle and not reliable on the basis of the single Chaclacayo specimen we examined.

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the species of *Dipsas* are usually regarded as highly arboreal, *Dipsas oreas* at the Rio Zaña site and other sites in northwestern Peru (personal observations; see also Orcés and Almendáriz, 1987) spends its inactive diurnal period in retreats within or under surface objects on the ground, or in holes in the ground, and ascends vegetation at night. Observations on *Dipsas peruana* at several sites in southern Peru suggest a similar behavior pattern. Orcés and Almendáriz (1987) reported a clutch of seven eggs of *D. oreas* beneath decomposing humid logs in Ecuador.

The second characteristic requires further comment, as it approaches the condition in *M. ataktolepis.* The specimen has a total of 34 medial dorsal scales between the occipitals and the posterior margin of the hindlimb, which is typical for the other *ruthveni* samples (Table 2). However, each of the enlarged rows is disrupted by the intercalation of small scales. That is, neither of these rows is continuously enlarged from the occipitals to the tail base. There are 14–16 enlarged medial dorsals anteriorly, followed by additional medial dorsals of varying sizes, some approximately the same size as the "enlarged" anterior scales, others much smaller. Furthermore, the larger and smaller of these posterior scales are intermixed within each medial dorsal row and have no consistent arrangement between the two rows. This condition is similar to that in *ataktolepis,* but in available specimens of that species the size reduction occurs only once, and small scales then continue to the tail base.

Given the unusual features of KU 220845 relative to other *Macropholidus ruthveni* we have examined, we defer an opinion about the taxonomic status of this population, which is currently under study by Antonio W. Salas and his colleagues. However, in addition to being widely disjunct from the other localities known for *ruthveni,* it is worth noting that Chaclacayo is about 500 m lower in elevation (889 m; Stiglich, 1922) than any other *ruthveni* localities, and the region is presently much more arid than the habitats at the other known localities for *ruthveni.*[6] Details microhabitat information and study of larger samples from this population should help clarify its systematic status.

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[6] In this context, the uncertain origin of the "Chongollapi" paratypes of *M. ruthveni* may be significant. Chongollape is a town of the coastal desert, and Noble only suspected that the paratypes came from higher, more mesic environments farther inland. We agree with this inference. Nevertheless, isolated populations of *ruthveni* or related species may exist in pockets of mesic or riparian habitats in the Peruvian coastal region. Well-documented specimens will be necessary to verify this possibility, which, in any event, we consider unlikely. However, species of the presumed closest relative of *Macropholidus, Pholidobolus,* inhabit mesic to xeric montane habitats in Ecuador (Montanucci, 1973:21); given the few documented localities for *M. ruthveni,* it may be premature to draw general conclusions about habitat specificity in this species.

STATUS OF *MACROPHOLIDUS* VIS-À-VIS *PHOLIDOBOLUS*

Noble (1921a:137) noted one point of similarity (lack of prefrontal scales) and one point of difference (presence of lateral scales of reduced size in *Pholidobolus*; uninterrupted lateral scales in *Macropholidus*) between *Macropholidus* and *Pholidobolus*. Species of *Pholidobolus* described subsequent to Noble's paper (Montanucci, 1973) showed that both characters are variable within *Pholidobolus*. With the discovery of *Macropholidus ataktolepis*, prefrontal scales are now known to be variably present in *Macropholidus*. Of the 16 nonosteological/nonhemipenial features used by Montanucci (1973:31) to define *Pholidobolus*, the two species of *Macropholidus* share all but the weakly keeled to striated dorsal scales. Dorsal scales of the tail in both species of *Macropholidus* may, however, be weakly striated. We have seen neither osteological nor hemipenial material of *Macropholidus*.

Macropholidus is further distinguished from all species of *Pholidobolus* by the two parallel series of enlarged dorsal scales, which are foreshortened in *M. ataktolepis*, and by having a translucent disk in the lower eyelid (but this feature is present in most specimens of *Pholidobolus annectens*; Montanucci, 1973:5). The two species of *Macropholidus* are smaller than any of the described species of *Pholidobolus* (maximum SVL for the largest specimens of *M. ruthveni* and *M. ataktolepis*, both females, 45.5 mm and 39 mm, respectively; maximum SVL for females of *Pholidobolus* ≥56 mm for all species [Montanucci, 1973]).

Macropholidus and *Pholidobolus* share one apparently derived scutellational feature: the presence of two median rows of enlarged gular scales (Kizirian and Coloma, 1991:420; this character is shared also with *Prionodactylus*). Thus, if this feature proves indicative of a close relationship between *Pholidobolus* and *Macropholidus*, as seems likely given their shared character suites and geographical distributions (see Cadle, 1991:85–89), then the enlarged dorsal rows characteristic of *Macropholidus* may be simply autapomorphic for these two species, and *Pholidobolus* may be paraphyletic with respect to *Macropholidus* (a similar interpretation of the lower eyelid disk might be possible, pending its eventual interpretation in *P. annectens*). Phylogenetic studies of the broader relationships among microteiids should clarify this issue.

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NOTES ADDED IN PROOF

1. Antonio W. Salas (personal communication) provided additional details concerning the Chaclacayo (Lima Department) population of *Macropholidus ruthveni* (p. 34). Specimens are known only from an artificial forest created in association with a resort establishment by plants imported from many other places and maintained by aggressive cultivation in this otherwise arid locale. Salas believes, and we concur, that the *ruthveni* population at Chaclacayo very likely resulted from introduction with these imported plants. If so, this would remove the distributional and microenvironmental anomaly produced by the record.

2. We recently collected specimens of *M. ruthveni* (to be deposited in MCZ and in the Museo de Historia Natural de la Universidad Antenor Orrego) from the vicinity of Sangal, Cajamarca Dept., Peru, 2000 m [07°08′ S, 78°50′ W], approximately 48 km SE (airline distance) of the Monte Seco population of this species; the new locality represents the southernmost population known for *ruthveni*. Specimens were collected under rocks in disturbed habitats (pastures, agricultural land, and brushy hillsides). Significantly, the Sangal population is only about 30 km north across the broad, dry valley of the Rio Chilete from the only known population of *ataktolepis* at Bosque Cachil. Thus, the distributions of the two species may be parapatric at the boundary formed by the Rio Chilete, or the ranges of the two species may approximate one another at appropriate elevations around the headwaters of this river (assuming adequate habitats remain in this highly populous region). Conceivably, the two species could even be sympatric in as yet undiscovered populations in this area.

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A COMPUTER APPROACH TO THE COMPARISON AND IDENTIFICATION OF SPECIES IN DIFFICULT TAXONOMIC GROUPS*

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AND ROBERT J. O'HARA[4]

ABSTRACT. A computer program for the identification of unknown taxa in "difficult groups" based on matching rather than sequential exclusion is proposed as a substitute for both the conventional dichotomous key and for the random entry matrix that has been suggested as a replacement for the dichotomous key. The matching program is modeled after the steps that a practicing taxonomist would employ in the identification of an unknown specimen:

1. Data for the unknown are compiled.
2. Data for the unknown are compared with those of relevant known taxa.
3. On the basis of the comparison, certain of the named taxa are considered possible matches with the unknown.
4. Final choice of the named taxon best matching the unknown is made and confirmed from additional data. If there is no match, the possibility of an undescribed species must be confronted.

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The program enables a computer to follow these steps:

1. It first enters the states of selected characters for the unknown individual or series. For each character of the unknown individual or series, two numbers are recorded, a minimum and a maximum; in the case of the series allowing for variation within the sample, and in the case of the individual allowing for differences between its two sides *and* also obscurities and ambiguities in counts or coding.
2. Once these data are entered, the program compares them against the ranges recorded in a reference matrix for selected known species. The user specifies the maximum number of characters in which a taxon in the reference matrix is allowed to differ from the unknown before being accepted as a "match."
3. The resulting report lists all the matching taxa and, for each, the number of characters not matched, the specific characters not matched, and by how much.
4. Included in the report for each matching taxon is a "descriptor" that cites characters that are not coded for the computer as well as characters regarded as "diagnostic" of the taxon. The descriptors assist in the final choice of the most plausible identification for the unknown. In certain cases (e.g., a new taxon), evaluation of the descriptors may require the user to reject all matches.

While the program was inspired by problems encountered during exploration of the systematics of anoline lizards, it does not deal with phylogeny at all. It is only—in our eyes—a *better* substitute for the dichotomous key. It aids in the identification of animals. As such, it has been customized for the anoles. The reference matrices, character descriptions, and "descriptors" provided as examples in the second and succeeding sections of this paper are for anoline lizards only. The concept of the matching program is, however, applicable to taxa of any sort.

I. HISTORICAL INTRODUCTION

Ernest E. Williams

Some years ago, while visiting Stanley Rand in Panama, I wondered aloud whether and to what extent computers could be used in species identification. I expressed dissatisfaction with the computer keys I knew about and with the usual dichotomous keys employed in taxonomic works in general. The dichotomous key did not at all resemble the process by which the working taxonomist, engaged, for example, in revising a large and complex genus, would actually employ to distinguish the species.

In my own work on anoline lizards, I had grown into the habit of using a standard data sheet for almost every anole specimen that I encountered, whether I recognized the species on sight or not, and very definitely for any specimen that I did not recognize

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with complete certainty. I routinely recorded museum number and locality and then a set of about 25 characters, some of them counts, sometimes brief descriptions, and, last of all, some very brief remarks on color as preserved. I used these data sheets to compel myself to always take the same data on all specimens and to standardize my information with regard to species that I did not know well. In the case of West Indian species, which ordinarily I knew in life, color, shape, and some scale differences that seemed diagnostic were the way that I distinguished species, but with mainland species that I knew only as museum specimens—and furthermore as specimens preserved, as the older specimens usually were, in ways that minimized color distinctions, and having scale characters that I had little acquaintance with—my data sheets seemed the only way to go.

My method of comparison for these unfamiliar species and characters was, however, primitive: a random, intuitive search for matching characters and populations. It seemed to me that there must be a way to automate the comparisons—the matching—that I was already doing by hand and that computers must be the best way to do this.

Not all of this do I know to have been said at one time, or even in one place, but it is certain that at one supper hour Stan Rand agreed with my general philosophy and, with his son Hugh's concurrence, voiced the opinion that a computer matching program of the sort that I imagined was feasible. By my visit the next year, Hugh Rand had written a Basic program for the Apple II computer that was the first version of the system described here. I provided the first reference matrix, one for Puerto Rican anoles. Stanley Rand emended the Apple II version and then created an IBM PC version, for which I have added matrices for Panamanian, Costa Rican, and Ecuadorian anoles to the one for Puerto Rico. This version is used at the Smithsonian Tropical Research Institute.

Much later, when Robert O'Hara was my assistant and especially my advisor-expert for the Macintosh computer, he introduced me to HyperCard, and using that very special application he created for me the Macintosh version that is also the database on which I work and from which I furnish the reference matrices used by the IBM PC.

II. A COMPUTER MATCHING PROGRAM FOR USE AS AN IDENTIFICATION KEY

Ernest E. Williams, Hugh Rand, and A. Stanley Rand

Difficult taxa are those for which none but the specialist can identify species with any confidence, and the specialist not without tremors of unease. They are typically large genera in which species distinctions are subtle or ambiguous. They may even be relatively easy to identify in one sex or under special conditions. Typically the species list is still very incomplete, and the possibility of encountering a new species is still uncomfortably high. These are taxa for which the dichotomous key may be as often a trap as an aid. It is our thought that a computer key of a novel type will be able to help where conventional dichotomous keys fail.

It was recognition of the difficulties associated with certain taxa that led Peters and Orejas Miranda (1970) and Peters and Donoso Barros (1970), in the two-volume *Catalogue of the Neotropical Squamata,* to present character matrices instead of dichotomous keys in three cases (the snake genera *Atractus* and *Bothrops* in Volume 1, and the lizard genus *Anolis* in Volume 2) and to advocate computer sorting. It is interesting to quote in full their reasons for doing so (pp. vi–vii, identically paginated in the snake and lizard volumes):

> "Most of the keys presented here are the standard dichotomous type . . . . In the case of very large genera, however, we have introduced a different concept. Any attempt at writing keys for poorly known large genera is likely to be futile, and we have avoided this by presenting as much data as possible in the form of a matrix. This permits 'random entry' identification, for the user, in the matrix that he wishes to check and eliminates all taxa that do not possess that character, finally arriving at a considerably reduced number of taxa (hopefully only one) after checking a series of characters. This concept has formed the basis of computer identification, since the machine can do such sorting more rapidly and efficiently than the human, and the random entry matrices presented here are organized in such a way that they can be incorporated in the computer programs now available for such machine sorting. It is our assumption that this method

> of identification will be used more and more in the future, and we hope that presenting these matrices will encourage others to begin to organize their data similarly, thus anticipating the day when computer keys are available to all users."

The matrices provided by Peters, Orejas Miranda, and Donoso Barros partly parallel the procedure we shall advocate below, but to our knowledge they have received little use. The sampling for the contained species was inadequate, a major problem for genera in which high individual variability is a characteristic. The data for our own matrices were collected from 20 specimens whenever possible and as many as are available in all other cases.

More fundamental, however, is a conceptual difference in method between the Peters, Orejas Miranda, and Donoso Barros approach and our own. Their method (and Peters advocated similar techniques in other papers; see Peters and Collette, 1968; Morse *et al.*, 1971) was to sort by *sequential exclusion*: i.e., by the fundamental technique of the dichotomous key, but here pursued by "random entry" with the aid of a computer. The goal of such a method is elimination of all but one of the possible choices, and no individual of a species is allowed to have the alternative of the successively chosen character. Our technique is the inverse of this: *matching,* instead of exclusion. Variation *and overlap* are expected, and the goal is *maximum congruence,* rather than elimination.

We have called our system a "key." It is certainly not a conventional "key," and, although it will assist in the identification of species, it is not at all comparable to a conventional dichotomous key. Instead, it is a computer-assisted procedure deliberately modeled after the steps that a taxonomist would employ in attempting the assignment of new specimens to the recognized taxa for which no dichotomous key existed. No taxonomist reviewing a large snake genus, for example, would begin by relying on the dichotomous keys prepared by his or her predecessors. The taxonomist would begin by collecting data—data on the number and, perhaps, shape of head scales; on the number of dorsal rows and ventrals; on the pattern on the head, body, and the tail; on sexual dimorphism, locality, and habitat; etc. Thereafter, the procedure would be to associate populations of phenetically similar animals, animals similar in detail, even if not identical, since nothing biological is exactly similar. The taxonomist would, in fact, be matching individuals and populations, determining in what regards and by how much the members of selected species might differ. Judgment would necessarily be involved. The expertise for which the experienced taxonomist is known is necessarily a familiarity gained over time with the chosen taxon. During this learning period, there grows an appreciation of which characters are most meaningful for species distinction or, at the least, the most readily determinable without major error. There comes also an appreciation of the kind and extent of the variation that seems to accord with the gaps that separate some underlying biological realities that are called "species."

The steps that the practicing taxonomist would use in the identification of a series of some unknown taxon for which there happened to be no conventional key would certainly be the following:

1. On the basis of prior experience, preliminary investigation, and/or literature search, characters are selected to be routinely checked in all specimens.
2. A table or data matrix is prepared recording the ranges of the states of the chosen characters in the named taxa to be compared.
3. The new specimens are examined for as many as possible of the chosen characters.
4. The table or data matrix is searched for matches and mismatches with the characters of the new specimens.
5. Tentative assignment of specimens to recognized taxa is made on the basis of closeness of match.
6. The tentative taxonomic assignment is confirmed or rejected with the aid of additional characters, whether from the literature or from previously determined specimens.

Our computer "key" breaks this procedure into two parts.

The *first part,* corresponding to steps 1 through 5, depends on *reference matrices* that contain codings for qualitative character states or standard counts, such as those that are (or should be) taken routinely on any specimen of the relevant taxa. These counts or character states are stored and compared by the computer with the data entered for specimens or series to be identified.

The *second part,* corresponding to step 6, is a supplementary set of species *descriptors* (automatically provided in the computer search report) that highlights the most valuable diagnostic features of each species and reports its known geographic range, ecology, behavior, or other significant features such as color in life.

Together these two data sets are intended to permit the "keying out" of all species presently known for any taxonomic group from any studied area. Importantly the program has three especially useful capabilities:

1. The program will report not only those species in the reference matrices that match the specimens or series under examination but also those that are similar. The computer will, in fact, ask the user of the key by how many characters the unknown may be allowed to differ.
2. The program will report how many and which of the characters do not match the coded data for species in the reference matrices and by how much they differ.
3. The program can be used to discover shared characters—whether plesiomorphic or synapomorphic—or combinations of shared characters of either kind simply by employing as the unknown the relevant character state or states and searching for those taxa that match.

More importantly, however, our computer key contains provisions for its own improvement. Built into the program are procedures such that both the reference matrices and the descriptors may be modified or expanded to include new or more useful characters or newly discovered species or species of other regions.

When new species are discovered, a dichotomous key can be very hard to change in ways that accommodate the new data. Often old dichotomies no longer work. The addition of the new species may require that the key be rewritten entirely, and this may be a job that compels reexamination of all the taxa involved. In contrast, in our program data matrices for the new species can easily be constructed and added to the reference set with no changes to the program itself or to the other reference matrices.

It is to be emphasized that this system routinely provides for variation and ambiguity. The expectation of variation is, in fact, built into the system. All character states or counts *must* be specified by two numbers. If the character state or count is monomorphic for any species, this fact is entered in the matrix by simple repetition of the coding number (e.g., 1,1 or 3,3). If there is variation between the two sides of an animal *or* within a population *or* if there is *intermediacy or ambiguity* in the assessment of a character state or count, then the two appropriate extreme numbers should be entered (e.g., 1,3 for a character state or 16,19 for a count).

There are caveats that need mention. Several negative features of our "key" are intrinsic to its concept and therefore irremediable without discarding the concept. These are as follows.

1. The computer accepts as a match the minimum or the maximum recorded in the matrix or any number that falls between these extremes. This results in three problems.

First, in the three characters that involve enlarged scales (characters 7, 14, and 21), coding has to deal with conditions ranging from 0 (no scales enlarged) to a condition in which there is a series of gradually enlarging scales that must be coded arbitrarily. We have chosen to code such gradually enlarging scales as 30,30 or 50,50. This means that any species or series of an unknown where some individuals have no enlarged scales and others have many very slightly enlarged scales, or any unknown in which the choice between these two is ambiguous might be coded 0,30. Any species with this coding in the reference matrix will be matched by any unknown with an intermediate coding for this character, and any unknown with this coding will match all species in the reference matrix on this character; i.e., there will be many false matches. The descriptors should resolve this difficulty. We advise the user to treat matches that involve these enlarged scale characters with caution.

Second, many species also have overlapping ranges for individual characters but, although the means may differ greatly, the computer will, of course, accept as a match to both species any value that falls within the zone of overlap. Because of this aspect of the program, individuals will often be unambiguously identified, whereas series, even when subjectively the same species, may not be. It must also be stressed emphatically that a report of zero difference by our program is *not* a statement of species identity. It is only a statement of zero difference in the chosen characters.

Third, in some cases zero differences appear to indicate true relationship, but many times species that are judged to be remote from one another on the characters *not* in the reference matrix are reported by our program as close or as exhibiting zero differences.

Remedies: In all cases of ambiguity on the initial run-through, recourse must be had—special consideration must be given to the *descriptors,* the second feature of our program, which cite such features as locality or color that are not readily computer-codable and that highlight special morphological, behavioral, or ecological traits.

Often the descriptors will eliminate taxa matched by the computer from further consideration. The excluded species may differ radically from the unknown in color or shape or in some other way not coded in the reference matrix. Alternatively, the descriptors may afford clear support for an identification by calling attention to or emphasizing very evident characters of the unknown—such as color, shape, or some feature special to the species. In any case, both tentative mismatches or matches should *always* be corroborated by examination of previously identified specimens and/or a check of the pertinent literature.

2. Instead of matching too many species, the unknown will sometimes not match any closely. If among the reference matrices there are unique types or small series, there will *ordinarily* be a failure to perfectly match a specimen or small series that, in the judgment of the inquiring systematist, should be conspecific. This is expectable. No unique biological specimen is ever exactly matched by another. In consequence, if any species is described from a single specimen, the identification of the next specimen is *always* a matter of extrapolation. A type or any unique specimen may set the universe of discourse, but it does not bound it. A type is an *example* only; it necessarily does not and cannot exhibit the range of variation that is contained in the population of which it is a member.

Remedies: In cases of failure to match any descriptor, the very real possibility of a new species will have to be confronted. Here, as in the case of too many matches, a conservative approach is appropriate.

Special consideration should be given in both the cases of too many matches and of no match at all to unique features of the unknown, whether it is an individual or a series. Decision, in any case, depends on differences between populations. A unique type or potential type needs to be compared with populations, optimally with relevant sympatric or adjacent populations. If the characters of any unique type or potential type fall within the set that is characteristic of a well-sampled population, and the descriptors do not exclude it, synonymy is the first and most probable decision. We say only probable decision, because, before any decision, every kind of error must be ruled out. In all cases, the characters reported in the descriptors need to be carefully scrutinized—in particular color, pattern, and geography, including sympatry or near sympatry, and habitat.

3. It will never be possible to code all characters of possible taxonomic significance. Some, like color, pattern, or body shape, are difficult to code for computer use unless broken down into fine details. Every taxon will have its special features, which may often be more readily expressed verbally rather than in computer code. Some of these features may be unique and make the species instantly identifiable. (This is, in fact, a danger, because unique and easily recognizable characters may often conceal even species differences among populations so easily recognized by one character that no further scrutiny is given them.)

The flexibility of our program should be strongly emphasized. It permits the distribution of single character states or of special combinations of character states to be tracked through entire taxa or subsets of them, making possible tests of the validity of old taxa or providing evidence for the erection of new taxa. In general, the system here presented will prove readily adaptable internally to individual needs. Certainly the system itself can be modified or superseded.

Some final statements should be made. First, our program provides no escape from matters of judgment. In the characters employed as well as the species recognized, human judgment has entered in. The program can only mechanically sort and match what human judgment has given it. The program will not, in any genuine sense, solve any taxonomic problems; it can, however, serve the purpose of calling attention to and exploring problems. One of us (EEW) now routinely uses it for the exploration of problems in the systematics of anoline lizards.

Second, it is important to emphasize that our program does not deal with phylogeny; it is a phenetic program, dealing with overall similarity. Homoplasy may often be a reason that species estimated to be remote phyletically may be reported with zero difference by our program. In such cases, rather than discovering true relationships, it discovers ecomorphs (Rand and Williams, 1969; Williams, 1972, 1983). However, it may also reveal the often subtle phyletic constraints that require differences between ecomorphs.

Finally, in the subsequent sections of this paper, the single example provided is one herpetological taxon, the anoline lizards. This is only an historical accident. The idea of a matching key arose, as recounted in Section I, among students of these peculiar and special animals. No feature of the fundamental concept of our system restricts it at all to this specific taxon. Other taxa and other environments may use our system.

For example, Knowlton (1993) has emphasized the abundance of sibling species (="difficult" genera) in marine environments. She cited this (p. 189) as due to "both inadequate study of morphological features of living organisms ('pseudo-sibling species') and divergence in habitat, life history, and chemical recognition systems without parallel divergence in morphology."

There is no reason not to extend this generalization to terrestrial systems. One of us (EEW) has been very aware in anoline lizards of "inadequate morphological study," including very inadequate and very incomplete descriptions of morphology. (The section in this paper that deals explicitly with anoline morphology is an attempt to describe some of the characters that should routinely be considered in every description of an anoline lizard. More can and should be added.) EEW has also been aware of habitat, life history, and visual (color and behavioral) recognition systems in anole lizards.

In the actual anoline matrices, only *external* morphological characters have been utilized. The ecological and color characters have been relegated to the descriptors. This is not at all a necessary action. It may not even have been a prudent one. *Any* codable feature, ecological, behavioral, skeletal, or biochemical, may be utilized by our system. We sincerely hope that our matching key will be utilized by students of marine organisms as well as by students of other terrestrial biota.

III. ANOLINE LIZARDS AS A TEST CASE FOR THE MATCHING KEY

Ernest E. Williams

The group first explored with the aid of our system is the anoline lizards, a monophyletic group that may include more than 400 species. We are able at this time to provide data for only limited segments of this chosen group. These small segments are provided only as examples and samples: examples of the method and samples simultaneously of some general problems and, of course, of the special features that must be tailored to each individual case.

The anoline lizards have inspired the development of our system because they fit so well into the category of difficult taxa. They have, indeed, traditionally been so regarded. In part—the most trivial part—this is a result of the high number of species. But, especially, the difficulty in identifying the anoles is a result of overlapping variability in scale characters and the absence or near absence of the invariant characters so necessary for the classic dichotomous key. The dearth of invariant characters is especially egregious for females and juveniles, and this by itself tends to make a dichotomous key inoperable.

In addition, the anoline lizards are highly visually oriented, and color vision is important in social interactions. Unfortunately, the importance of color in life to the animals themselves does not at all help in sorting out preserved specimens. Species often differ very little in any external feature except color, yet the usual methods of preservation obliterate or obscure characteristic colors and patterns or, alternatively, reveal patterns unusual in the live animal. The colors of the living animal are always more or less altered and may be darkened in poorly preserved specimens of many species to a uniform muddy brown. The dewlap, it is true, is usually much less altered, and especially less darkened, than other portions of the body, but it is much more often than not quite absent in females and, unless preserved fully extended, is of little use even in males. Furthermore, even live animals may differ greatly in color or pattern according to physiological and psychological states. It is therefore small occasion for surprise that keys that rely heavily on color characters in anoline lizards are less than universally useful.

This is true, unhappily, for our matching program as much as for dichotomous keys. For species distinguished primarily on color characters, many formaldehyde-preserved specimens are useless. Our matching program may, indeed, be able to do more than the conventional dichotomous key: the 37 external characters that are used in the key may sometimes achieve identification when color, because of artifactual uniformity, fails entirely. But even scales may be poorly visible on badly preserved specimens, and it should be emphasized that old specimens of anoline lizards that are uniformly brown or black as preserved, without information on colors in life, or dry, damaged, or inadequately preserved are, for many or most purposes, worthless.

So species-rich and widely distributed a taxon as the anoline lizards is for many purposes unmanageable as a unit. Since Boulenger's key of 1885—never very useful and now, in the most genuine sense, hopelessly out of date—no dichotomous key for the anoline lizards has ever existed, nor is one ever likely to exist. It is the plausible practice of the taxonomist to break such a large unit into smaller segments, at least geographically, perhaps by political boundaries, or perhaps by presumed or provisional "natural" units. Even the computer system that we propose will work most usefully and easily on smaller units than the 400 *or more* species that is the expected total for the whole taxon.

As a first—but, we feel, a fair—test of our system, we have tried it on the 12 species occurring on the Puerto Rican bank: the land area exposed at various times during the Pleistocene of which Puerto Rico and the Virgin Islands and a few other small islands are the present emergent parts. Eleven of the species are unquestionably valid, ten of them—all those of mainland Puerto Rico—widely overlapping geographically or intimately interdigitating. The eleventh (*A. roosevelti* Grant) is rare or extinct, known only from six specimens. It was, indeed, known from only two individuals, until the recent reexamination of old collections. It is, however, distinctive enough that its species status has never been questioned. A twelfth species, *A. ernestwilliamsi,* recently described (Lazell, 1983), has a very small range, a single cay, an enclave within the range of its very widely distributed closest relative; its status is still disputed. Indeed, only the latter is a problem species in the sense that its species status *can* be questioned; all other species are somewhere sympatric with their closest relatives, *A. cuvieri* and *A. roosevelti,* which are allopatric and are distinguished by strong and consistent morphological features.

The twelve species include several species groups and range from siblings to taxa, the relationships of which, at least within Puerto Rico, are quite unclear. Small as the anole fauna of the Puerto Rican bank is, it will exemplify many of the problems of "difficult" taxa.

The anoles as a group cannot be specified by any single character nor by any unique combination of characters. The group is specified by the combination of two or three characters, any one of which may be missing. Again, it is usual, or at least not infrequent, that subgroups within the anoles present the same problem of definition. We suggest that this is the sort of difficulty that makes "difficult" taxonomic groups difficult. The special case of Puerto Rican anoles is in some regards an atypically favorable case. There are no known hybrids and no equivocal species except the one that has an extraordinarily restricted geographic range. Using both data sets, there should be in the case of the Puerto Rico anoles *no* specimens for which the determination is doubtful. There is negligible probability of the discovery of new species. This will not be true for other geographic segments of the anoline lizards. For these, there will be other problems to confront case by case. For example, in the case of the Panama–Costa Rica matrix, we know of at least nine Panamanian species that are undescribed and one or two others that are possibly valid; we would also add to species recognized by Savage for Costa Rica some that he has synonymized or left undescribed. The existence of undescribed or disputed species is a very general problem in all the Central American and South American areas of anole distribution. Only Cuba presents many similar issues in the West Indies.

IV. THE MORPHOLOGICAL CHARACTERS USED IN THE ANOLEKEY DESCRIBED, DEFINED, AND ILLUSTRATED

ERNEST E. WILLIAMS

The 37 counts and character descriptions provided in the matrices used by the IBM and Macintosh ANOLEKEYs have been chosen by myself as those believed, after long trial, to be the most useful examined and *readily codable* characters (size, proportions, scale character states, and counts) for anoline lizards as a whole. This is a personal judgment and perhaps a very temporary one. It can be justified only by some measure of empirical success, and it remains to be widely tested.

The following counts and character states are presented as a coded sequence of alternatives (Table 1). It will always be possible, and often probable, that counts a little higher than or states adjacent to those presented for any species in the coded matrix will be found in a specimen presented for identification. In considering whether to accept a match or a failure to match in an ANOLEKEY Report, allowance should always be made for this possibility. However, counts or conditions numerically farther away from those predicted by the matrix for the species found closest to the examined material on first trial should be regarded as evidence for preferring the identification of some other species. Certainly this is grounds for reexamining, perhaps recoding, some of the characters of the unknown anole and, as well, very carefully considering the alternative possibilities suggested by the supplementary *descriptor* provided for each matched species in the report.

It may well be that many current species matrices will require modification with an increase in sample size. (Those matrices based on samples below 20 will certainly need modification.) But such modifications should, of course, only be done *if* there is strong evidence from the congruence of the other characters *and* the details provided by the descriptor that the specimen with the discrepant character really belongs to the same species.

In such cases of failure to match the likelihood of a new species is especially real for the anoles of mainland South and Central America. Both areas are inadequately known, and local new spe-

Table 1.

1. Head Scales. Smooth: 1,1. Rugose: 2,2. Unicarinate: 3,3. Multicarinate: 4,4. Striate: 5,5.
2. Scales between Second Canthals (Fig. 1). 1–30.
3. Postrostrals (Figs. 1, 2, and especially 3). 2–15.
4. Nasal (Figs. 1, 2, and especially 3). Circumnasal: 0,0. Anterior nasal: 1,1. Divided anterior nasal: 2,2. Inferior nasal 3,3.
5. Scales between Nasal and Rostral (Figs. 1, 2, and especially 3). 0–5.
6. Scales between Supraorbital Semicircles (Fig. 1). 0–10.
7. Enlarged Scales in Supraocular Disk (Fig. 1). 0–30.*
8. Elongate superciliaries (Figs. 1, 2, and 4). 0–7.
9. Superciliary Series (Figs. 1, 2, and 4). Granules: 1,1. Small scales: 2,2. Larger square or swollen scales: 3,3.
10. Loreal Rows (Fig. 2). 1–15.
11. Loreal Number (Fig. 2). 2–40.*
12. Interparietal Relative to Ear (Figs. 1, 2, and 5). Much smaller: 0,0. Smaller: 1,1. Equal to: 2,2. Larger: 3,3. Much larger: 4,4. Interparietal absent: 5,5.
13. Scales between Interparietal and Semicircles (Fig. 1). 0–15. In the absence of an interparietal: 888,888 in the IBM version, NA in the Macintosh version.
14. Scales between Interparietal and Nape Scales (Fig. 1). In the absence of an interparietal: 888,888 in the IBM version, NA in the Macintosh version. Count of enlarged scales behind the interparietal distinctly larger than nape scales: 0–15. Scales behind interparietal grading into nape scales: 50,50.*
15. Scale Rows between Suboculars and Supralabials (Fig. 2). 0–3.
16. Supralabials to below Center of Eye (Fig. 2). 4–15.
17. Postmentals (Fig. 6). 1–15.
18. Sublabials (Fig. 6). 0–2.
19. Sublabials in Contact with Infralabials (Fig. 6). 0–10.
20. Dorsals (Figs. 7A, B). Flat, smooth: 1,1. Swollen: 2,2. Unicarinate: 3,3. Multicarinate: 4,4. Triangular or conical crest scales: 5,5.
21. Enlarged Middorsal Rows (Figs. 7A, B). 0–30.*
22. Middorsal Crests (Fig. 7A). None: 0,0. Low crest: 1,1. High crest: 2,2.
23. Flank Scales (Figs. 7A, B). More or less widely separated: 0,0. Juxtaposed: 1,1. Imbricate: 2,2. Heterogeneous: 3,3.
24. Size of Ventrals Relative to Dorsals (Figs. 7A, B). Larger: 1,1. Equal: 2,2. Smaller: 3,3. Much smaller: 4,4.
25. Smooth/Keeled Ventrals (Figs. 7A, B). Smooth: 1,1. Weakly keeled: 2,2. Strongly keeled: 3,3.
26. Ventrals (Figs. 7A, B). Separated: 0,0. Juxtaposed: 1,1. Subimbricate: 2,2. Imbricate: 3,3.
27. Toe Pads (Figs. 8A, B). Pad overlapping first phalanx: 1,1. Pad not distinct from first phalanx: 2,2. No pads: 0,0.
28. Lamellar Number (Figs. 8A, B). 0–50.
29. Supradigitals. Smooth: 1,1. With indistinct or single keels: 2,2. Multicarinate: 3,3.

TABLE 1. Continued.

30. Tail (Fig. 9). Round: 1,1. Weakly compressed: 2,2. Strongly compressed: 3,3.
31. Tail Crest (Fig. 9). None: 0,0. Serrate: 1,1. Distinct crest: 2,2. High crest: 3,3.
32. Postanals. Present: 1,1. Obscure: 2,2. Absent: 3,3.
33. Dewlap (Male) (Fig. 10). Large: 1,1. Intermediate: 2,2. Small: 3,3. Absent: 4,4.
34. Dewlap (Female) (Fig. 10). Large: 1,1. Intermediate: 2,2. Small: 3,3. Absent: 4,4.
35. Snout–Vent Maximum (Male): 0–300.
36. Snout–Vent Maximum (Female): 0–300.
37. Tail Length/Body Length: Ratios between 0.8 and 1.2: 1,1. Ratios between 1.3 and 1.7: 2,2. Ratios between 1.8 and 2.2: 3,3. Ratios between 2.3 and 2.7: 4,4. Ratios between 2.8 and 3.0 or more: 5,5.

*The last number is an arbitrary number (see text).

cies are rather to be expected than not. Only widespread common species are well known, and these only relatively so. This is not true for the anoles of the West Indies, which have been extensively studied, although Cuba, which has been relatively neglected, may be expected to have some efflorescence of novelties.

It is important to realize that the samples for even the best represented species have been selected opportunistically. When readily available, males, females, and juveniles have all been counted and coded, but no attempt has been made to secure a "fair" representation of age and sex classes. Sampling of geographic variation also has been opportunistic: no provision has been made for "adequate" sampling of described subspecies.

It is a matter of course that for poorly known species the samples are always biased and inadequate. There is always, as we have stated in Section II of this paper, extrapolation—judgment—in the association of a second specimen with a unique type or in the association of a population from a new locality with a species previously known from a small, geographically limited range.

It is important to reemphasize that there is no escape from such matters of judgment. Indeed, some of the species in our ANOLEKEY matrices may be composite. Named subspecies have been consciously lumped in the preparation of the reference matrices for the ANOLEKEY. Some subspecies will, rather surely, be recognized as full, valid species. Others will turn out to be biologically meaningless. We do not attempt to solve such taxonomic problems. We do provide a computer method that will assist the needed comparisons.

The ranges for counts reported in Table 1 as the permissible limits for counts or measurements may deliberately extend beyond the limits actually known for any anole species. Thus, the lowest known count of total number of loreals (character 11, later) is three (in two species of *Phenacosaurus*). I have coded the minimum number for total loreals as two, because this would be a readily expectable variation. Similarly, although the maximum count for lamellae under phalanges ii and iii of the fourth toe (character 28) that I have actually counted is 44, I have coded the maximum for this count as 50. Coding of this kind has been done in several characters in the interest of allowing for easy modification of matrices when known counts are exceeded in either direction.

In the case of character states, Table 1 reports the known states for each character, or, as in the preceding case of certain quantitative characters, extrapolated, to take care of variation that may become known in the future. Any state other than those listed must be coded 888,888 for the IBM version of ANOLEKEY, or NA (nonapplicable) for the Macintosh version. Any known character state not reported in some individual species matrix but found in some specimen judged to be conspecific with that species may be added to the appropriate matrix by use of the Change Menu in the IBM ANOLEKEY or by simple insertion of the missing coding in the relevant field in the Macintosh *Anolis Handlist.*

Certain counts are more repeatable than others, and some character states may not be readily interpretable. There should be, for example, except for obvious pathological conditions, no equivocal counts for the number of postrostral scales or for the number of scales between the supraorbital semicircles. In other cases, it is very necessary to be aware of arbitrariness and subjectivity in the evaluation of a character. Whenever this is true, advantage should be taken of the program's explicit recognition of the possibility of intermediacy or ambiguity in counts or character states by coding a range even for an individual. In all difficult cases, no time should be wasted by attempting false precision. Code intermediacy, if that seems appropriate, or code the extremes allowed by differing interpretations.

A special case exists in the several instances of graded series of enlarged scales. It is always difficult to decide when to count a scale as enlarged except in the cases of truly abrupt enlargement. In such cases, high counts often reflect a condition much closer to zero than to low counts. I have in such cases used arbitrary high numbers as signals that gradation in size has made counts subjective enough to be meaningless except as indicating gradual change in size.

In the attempt to facilitate the examination of specimens, counts and characters are listed in an order in which a specimen might readily and naturally be examined, beginning with the head and proceeding to the body, limbs, and tail.

Remember that all characters must be recorded by two numbers and that there must be a comma between the numbers. Missing characters should be coded 999,999 in the IBM version, or UA (=unavailable) in the Macintosh version. Nonapplicable characters should be coded 888,888 in the IBM version, or NA (=not applicable) in the Macintosh version. I explicitly reinforce the preceding admonitions by repeating in the coding for character states below double numbers separated by commas.

All terms used in Character Descriptions are defined in Peters' (1964) *Dictionary of Herpetology.*

Character Descriptions

1. *HEAD SCALES. Smooth:* ***1,1.*** *Rugose:* ***2,2.*** *Unicarinate:* ***3,3.*** *Multicarinate:* ***4,4.*** *Striate:* ***5,5.*** Recognition of smooth, more or less parallel ribbed (striate) or rugose head scales or those with strong single ridges (unicarinate) or strong multiple ridges (multicarinate) should not be difficult. The coding for any individual specimen should reflect the most extreme condition in terms of keeling. (The supraoculars may be the most useful scales to look at.)

A very useful character. Striate is the rarest condition.

2. *SCALES BETWEEN SECOND CANTHALS (Fig. 1). Range:* ***1–30.*** Because they are better defined posteriorly, the canthals are counted from the eye forward. The first canthal always

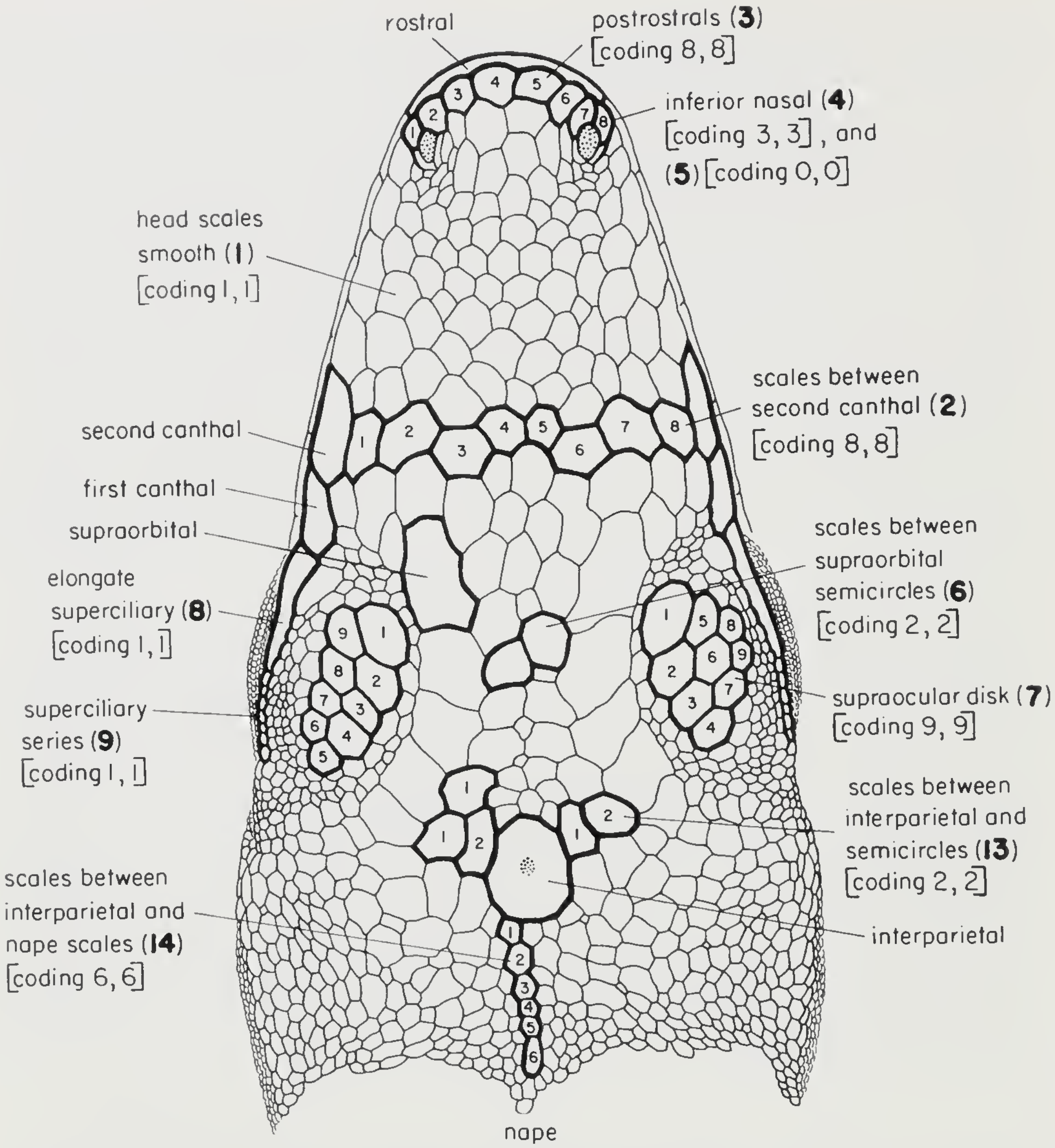

rostral
postrostrals (3) [coding 8, 8]
inferior nasal (4) [coding 3, 3], and (5) [coding 0, 0]
head scales smooth (1) [coding 1, 1]
scales between second canthal (2) [coding 8, 8]
second canthal
first canthal
supraorbital
scales between supraorbital semicircles (6) [coding 2, 2]
elongate superciliary (8) [coding 1, 1]
supraocular disk (7) [coding 9, 9]
superciliary series (9) [coding 1, 1]
scales between interparietal and semicircles (13) [coding 2, 2]
scales between interparietal and nape scales (14) [coding 6, 6]
interparietal
nape

Figure 1. Dorsal view of head of "typical" anole (characters 2–9, 13, and 14). Boldface numbers in parentheses indicate relevant characters; plain numbers in brackets display codings for the illustrated character states.

extends from the canthal ridge backward over the orbit; the second usually does not have such an extension.

This is not necessarily an easy count to make. Variation accounts for some of the problem. At the lower range of counts, variation within a species should not exceed 1 or 2, but it may be 4 or more at the higher extremes. Because two or more scales may be in contact with the second (or the third) canthal on each side, counts within one individual by different observers or by

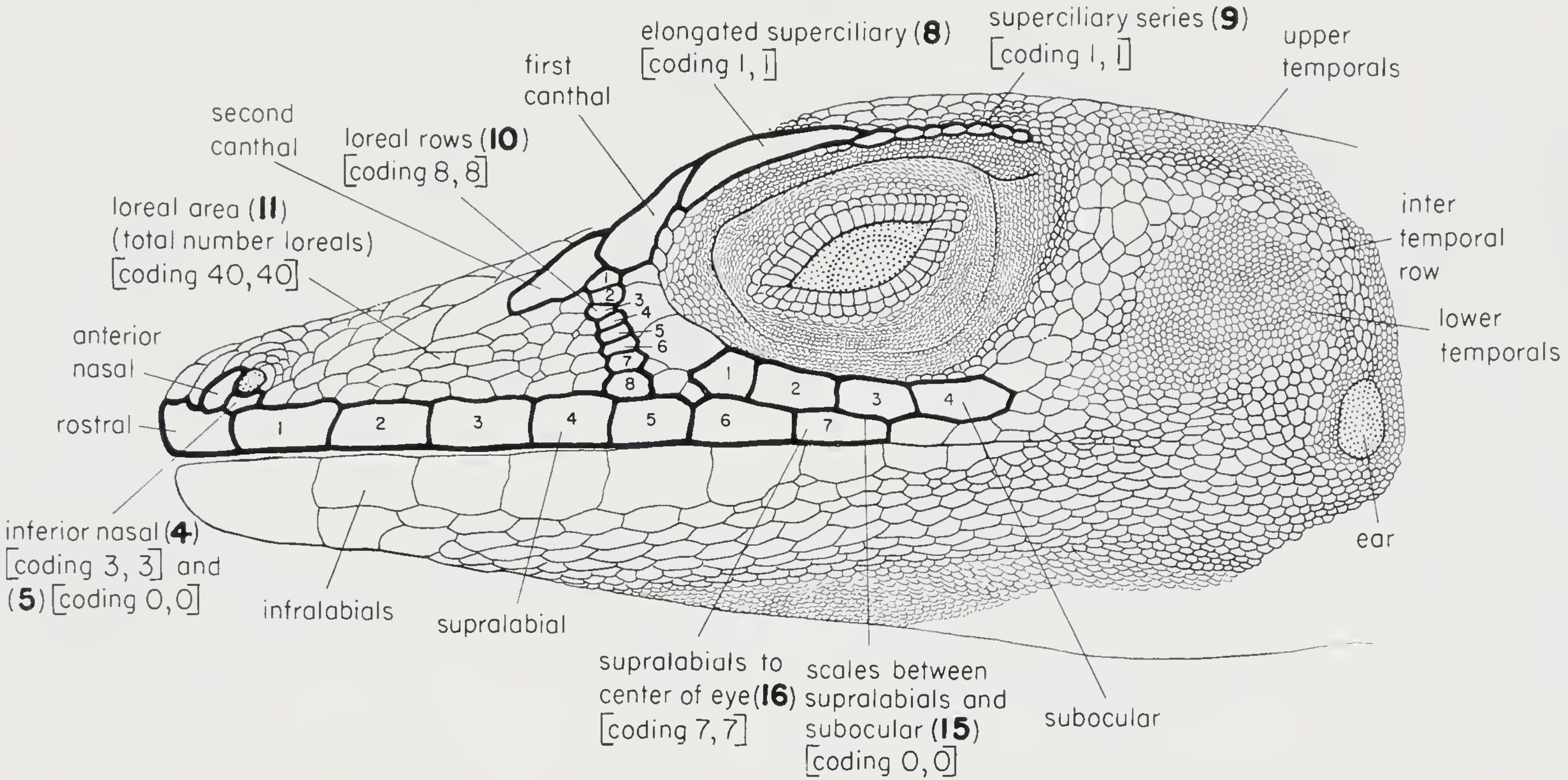

elongated superciliary (**8**)
[coding 1, 1]
superciliary series (**9**)
[coding 1, 1]
upper temporals
first canthal
second canthal
loreal rows (**10**)
[coding 8, 8]
loreal area (**11**)
(total number loreals)
[coding 40, 40]
inter temporal row
lower temporals
anterior nasal
rostral
inferior nasal (**4**)
[coding 3, 3] and
(**5**) [coding 0, 0]
infralabials
supralabial
supralabials to center of eye (**16**)
[coding 7, 7]
scales between supralabials and subocular (**15**)
[coding 0, 0]
subocular
ear
1
2
3
4
5
6
7
8

Figure 2. Lateral view of head of "typical" anole (characters 4, 5, 8–11, 15, and 16). Boldface numbers in parentheses indicate relevant characters; plain numbers in brackets display codings for the illustrated character states.

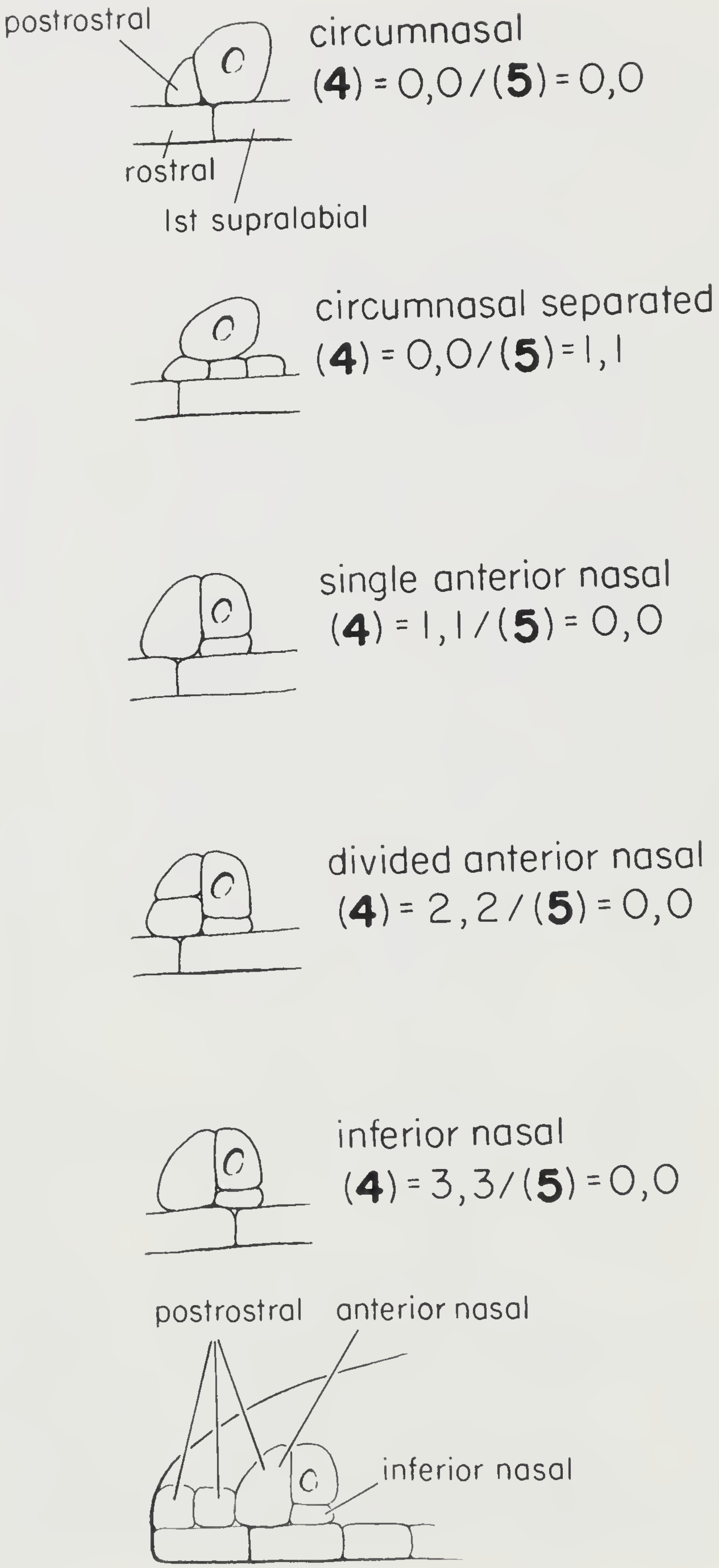

postrostral
circumnasal
(**4**) = 0,0 / (**5**) = 0,0
rostral
Ist supralabial
circumnasal separated
(**4**) = 0,0 / (**5**) = 1,1
single anterior nasal
(**4**) = 1,1 / (**5**) = 0,0
divided anterior nasal
(**4**) = 2,2 / (**5**) = 0,0
inferior nasal
(**4**) = 3,3 / (**5**) = 0,0
postrostral
anterior nasal
inferior nasal

Figure 3. Characters 4 and 5 (nasal scales of anoles).

one observer at different times may differ by 1 or more scales. For matrices based on few specimens, this may not be a useful character; it is primarily useful for the low counts, 2–5, but every species has a characteristic range of counts.

3. POSTROSTRALS (Figs. 1, 2, and especially 3). Range: ***2–15.*** Those scales behind the rostral, in contact with it, and between the supralabials are easily counted and will usually not vary within a species by more than 2 to 3. This count may include the circumnasal and any other of the differentiated nasals discussed next.

4. NASAL (Figs. 1, 2, and especially 3). Circumnasal: ***0,0.*** *Anterior nasal:* ***1,1.*** *Divided anterior nasal:* ***2,2.*** *Inferior nasal:* ***3,3.*** The nasal in anoles may be a single oval scale that contains the nostril. It is then coded as "circumnasal": 0,0. More often, the scales around the nasal are differentiated, overlap, and at least partially obscure it. Most common is a condition in which a scale anterior to the nasal becomes large and subtriangular and overlaps part of the nasal scale; it is then coded as "anterior nasal": 1,1. In some species, the anterior nasal is divided transversely; it is then reported as a "divided anterior nasal": 2,2. The other scales overlapping the nasal are not considered, except that the inferior nasal—a scale obscuring the lower surface of the nasal—if it comes to overlie the sulcus between the rostral and the first supralabial, is then, and only then, coded "inferior nasal": 3,3. Occasional anomalies (e.g., an anterior nasal replaced by small granules) or conditions due to injury should always be reported as 888,888 in the IBM version, or NA in the Macintosh version.

This and the next (character 5) are important and very useful characters. In some cases both may be difficult to score. It is then best to code the alternatives; these may have been already included in the relevant matrices.

Note that the sulci bounding the scales surrounding and overlapping the nasal are sometimes obscure and that, therefore, the existence, for example, of the anterior nasal must be inferred. Most often, the plausible coding will be 1,1. These difficulties should, in any event, exist only in single specimens or one side of a single individual. Series should obviate or alleviate the problem.

5. SCALES BETWEEN NASAL AND ROSTRAL (Figs. 1, 2, and especially 3). Range: ***0–5.*** In anoline lizards with the condition

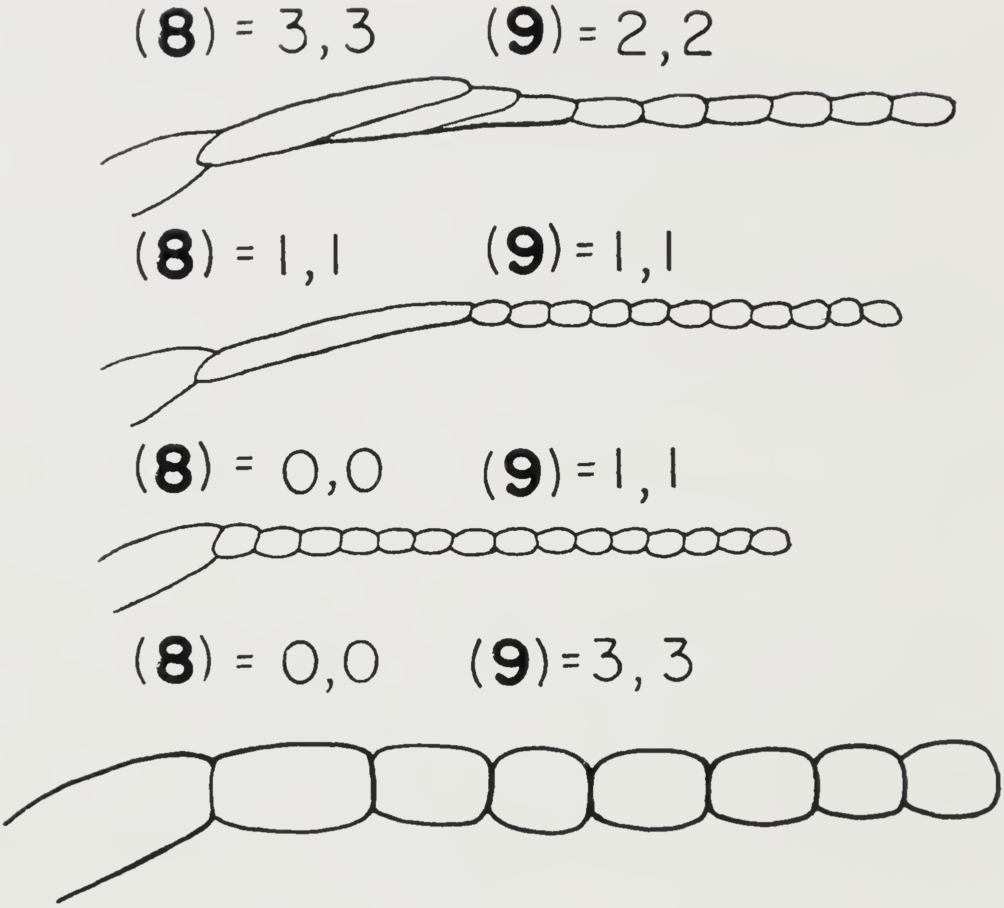


Figure 4. Characters 8 and 9 (superciliary scales in anoles).

"circumnasal"—the simple unmodified nasal scale—that scale may be in contact with the rostral, but one or more scales usually intervene. In the latter case, the minimum number is coded. In the condition "anterior nasal," the nasal itself is obscured, but the anterior nasal is usually in contact with the sulcus between the rostral and first supralabial. This condition is coded 0,0. If the anterior nasal is wholly in contact with the rostral, and the inferior nasal has moved into a position above the sulcus between the rostral and first supralabial, the coding is still 0,0. If, however, a recognizable circumnasal or anterior nasal is separated from the rostral by one or more scales, then the relevant minimum count is recorded.

Often more than one interpretation of any individual condition may be possible. It is, for example, difficult in some species to decide whether the nasal scales are properly regarded as the "anterior nasal" separated by one scale from the rostral (i.e., character 4: 1,1; and character 5: 1,1), or whether the better interpretation is "anterior nasal" divided and in contact with the rostral (i.e., character 4: 2,2; and character 5: 0,0). Ordinarily the ambiguity will already be recorded in the matrix for the species in question, and either of the options will be accepted by the computer.

6. *SCALES BETWEEN SUPRAORBITAL SEMICIRCLES (Fig. 1). Range:* ***0–10.*** This is a minimum count. Any contact, even a point contact, between the supraorbital semicircles is coded as 0,0.

This is an important count, but in some species there is exceptional variation.

7. *ENLARGED SCALES IN SUPRAOCULAR DISK (Fig. 1). Range:* ***0–30.*** Enlarged scales arranged as a supraocular disk may be conspicuously larger than any surrounding scales; they are then easily countable. In many species, however, there is gradation such that all counts are subjective; in such counts, a range should be reported. In still other species, the enlargement is so gradual and so limited that there can be no pretense of an accurate count. These cases should be coded arbitrarily as 30,30. If there is no indication of a disk or of significant enlargement of any of the supraocular scales, the coding should then be 0,0.

In many or most species of anoles, this is not the most useful of characters. It is useful in those cases that are unambiguous, i.e., those in which the disk consists of a few large scales that are sharply distinct from surrounding scales. High counts, i.e., smaller scales, are ordinarily subjective.

It is possible to be undecided about whether the coding should be 30,30 or 0,0. Specimens or species in which this occurs should be coded 30,30. The alternative, 0,30, is unacceptable, because the computer will then assume that all counts between 0 and 30 are valid, although no species is known in which so highly variable a condition is true. This coding will be closer to reality.

If you have before you any series containing low counts (large scales; e.g., 3–7) in the supraocular disk and also high counts (small scales; e.g., 20–30), that series should be suspect as composite, and low- and high-count specimens treated separately.

8. *ELONGATE SUPERCILIARIES (Figs. 1, 2, and 4). Range:* ***0–7.*** The superciliaries are distinguished from the canthals by not

extending anteriorly beyond the orbit at all. The first superciliary in anoles is usually distinguishable from more posterior superciliaries by being much longer anteroposteriorly. If there is more than one elongate superciliary (there may be as many as six), they will be strongly overlapping and grade in length posteriorly. In a few species, there is no elongate superciliary, and all the superciliary scales are granular. If so the coding is 0,0.

9. SUPERCILIARY SERIES (Figs. 1, 2, and 4). Granules: ***1,1.*** *Small scales:* ***2,2.*** *Larger square or swollen scales:* ***3,3.*** The scales posterior to the elongate superciliaries—if any are present—may be granular, like the smaller scales of the supraocular area, and are then coded 1,1. Alternatively, there may be one or two rows of distinctly larger but still small scales following the elongate superciliary or superciliaries. If there is difficulty in deciding between these two conditions, or if there is a mixture of granules and small scales, the code should be 1,2. If there is no elongate superciliary and all superciliaries are large and squarish or large and swollen, the conditions should be coded 3,3. The large and squarish and the large and swollen superciliaries are rare conditions, known only in two species in Colombia, Ecuador, and Panama.

10. LOREAL ROWS (Fig. 2). Range: ***1–15.*** Loreal rows are counted down from the second canthal or from the first canthal, if it clearly overlaps the loreal area (those scales that continue the subocular arc in front of the eye are preoculars, not loreals, and should never be counted). Sometimes, however, it is difficult to distinguish the preoculars from the loreals; this count is then subjective, by one or two.

This is a count that is often subjective. The next character (total loreal number) is then more useful.

11. LOREAL NUMBER (Fig. 2). Range: ***2–40.*** Total loreal number is easily counted when the loreals are few and the suboculars broadly in contact with the supralabials. Difficulty occurs when the loreals are confluent with a scale row or rows separating the subocular and supralabials. Whenever such a row is complete, the number of loreals will, in most cases, be relatively high (significantly >30); it is then convenient to use the arbitrary coding 40,40. In some cases the preoculars also may be difficult to distinguish. Where the total count would in any case be less than

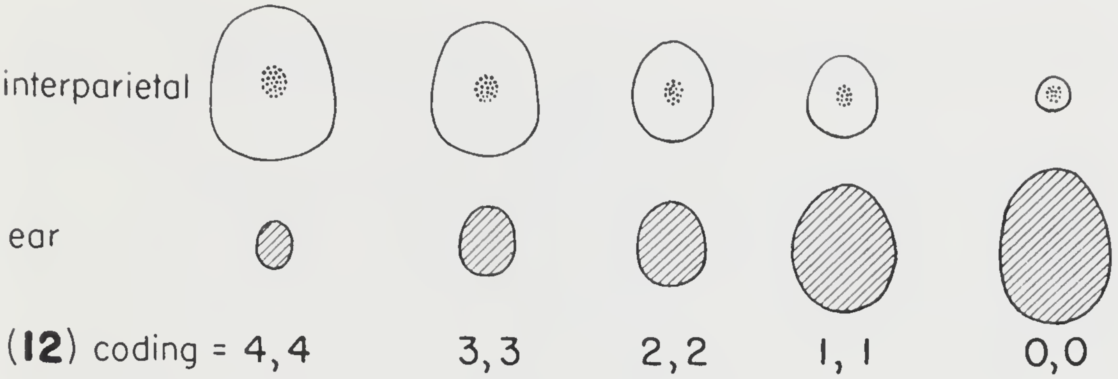


Figure 5. Size of interparietal compared with that of ear (character 12).

40, the possible interpretations may be coded as a range. If the ambiguous situation involves a high count, the arbitrary number 40,40 may be the best solution. Low counts are clearly diagnostic for certain species; even errors of one or two do not matter. High counts do not appear ever to be useful for species discrimination.

12. INTERPARIETAL RELATIVE TO EAR (Figs. 1, 2, and 5). Much smaller: ***0,0.*** *Smaller:* ***1,1.*** *Equal to:* ***2,2.*** *Larger:* ***3,3.*** *Much larger:* ***4,4.*** *Interparietal absent:* ***5,5.*** The size of the interparietal relative to the size of the ear is ordinarily unambiguous. If there is ambiguity or variation within a species, code as a range (e.g., 1,3). Again extreme conditions tend to be diagnostic, but in many species codings of 1, 2, or 3 will be appropriate within a single population.

The absence of an interparietal is a rare and apparently derived condition; it is confined to certain species in northwestern South America.

13. SCALES BETWEEN INTERPARIETAL AND SEMICIRCLES (Fig. 1). Range: ***0–15.*** *In the absence of an interparietal: 888,888 in the IBM version, NA in the Macintosh version.* If there is no interparietal, the coding of this character must be 888,888 for the IBM version, or NA in the Macintosh version. This is again a minimum count taken on each side from the interparietal to the nearest scales of the supraorbital semicircles. If the two sides differ, code them as, for example, 2,3. Ranges of 3 or 4 or more are not unusual in certain populations.

14. SCALES BETWEEN INTERPARIETAL AND NAPE SCALES (Fig. 1). In the absence of an interparietal: 888,888 in

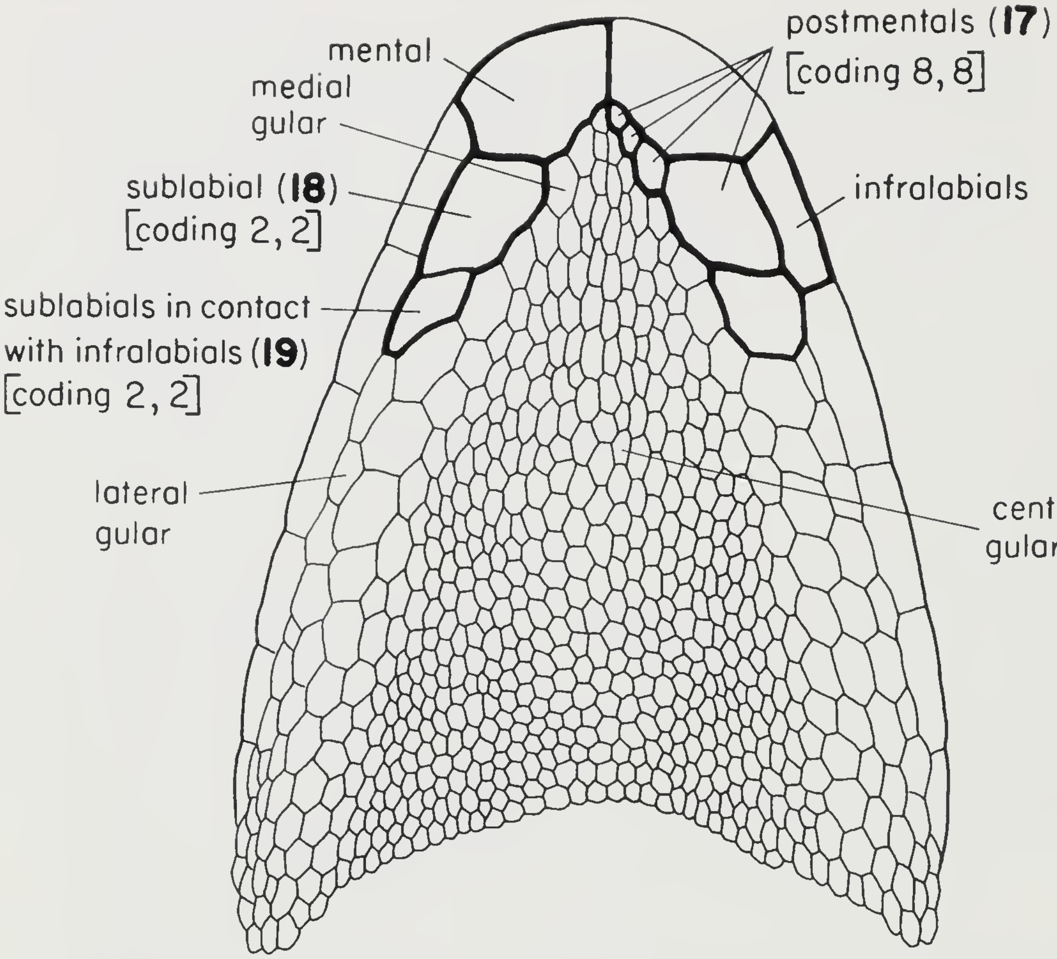

mental
medial gular
sublabial (**18**) [coding 2, 2]
sublabials in contact with infralabials (**19**) [coding 2, 2]
lateral gular
postmentals (**17**) [coding 8, 8]
infralabials
central gular

Figure 6. Ventral view of head of "typical" anole (characters 17–19). Boldface numbers in parentheses indicate relevant characters; plain numbers in brackets display codings for the illustrated character states.

the IBM version, NA in the Macintosh version. Count of enlarged scales behind the interparietal distinctly larger than nape scales: ***0–15.*** *Scales behind interparietal grading into nape scales:* ***50,50.*** This count is made in the approximate midline behind the interparietal, and the scales must be appreciably larger than the nape scales immediately behind them. If there is gradation, and this frequently is the case, the count is surely subjective. If so, code as 50,50.

Discrepancy compared with a matrix is not to be taken seriously in the case of high and subjective counts. However, 0 may have a taxonomic meaning, i.e., an interparietal followed by small scales not significantly different from nape scales. This differs importantly from cases in which scales behind the interparietal differ abruptly in size from nape scales. Thus, both a low count and an unambiguous count of 0,0 may be very useful species characters.

15. SCALE ROWS BETWEEN SUBOCULARS AND SUPRALABIALS (Fig. 2). Range: ***0–3.*** This is also a minimum count. *Any* contact between suboculars and supralabials is coded 0,0.

16. SUPRALABIALS TO BELOW CENTER OF EYE (Fig. 2). Range: ***4–15.*** Because the posterior termination of the supralabial series may sometimes be difficult to determine, the supralabials are counted from the rostral posteriorly. The sulcus between two supralabials may lie below the center of the eye. The coding is then a range (e.g., 6,7).

17. POSTMENTALS (Fig. 6). Range: ***1–15.*** This is a count of all the scales in contact with the mental between the infralabials. It includes the anteriormost sublabials, if these are differentiated.

18. SUBLABIALS (Fig. 6). Range: ***0–2.*** A sublabial series is an abruptly enlarged series of scales on each side paralleling or radiating from the infralabials. Abruptly enlarged is here interpreted to require that the first sublabial of each side be at least four to five times the size of the postmental (=medial gular) medial to it. If no such abruptly enlarged scales adjacent to the infralabials exist (i.e., if the postmentals are subequal or grade evenly from larger laterally to smaller medially), or if the enlarged scales are only twice to three times any medial gular, the condition is to be reported as the absence of sublabials, coded 0,0. If both first sublabials are present, the coding is 2,2. If, as sometimes happens, a first sublabial is present on one side only, the coding is 1,1. If there is ambiguity (i.e., if you cannot decide whether or not the putative sublabials are as much as four times the other postmentals), code 0,2.

This character again is a very useful one. If the sublabials are recognized only when the lateral postmentals are four to five times larger than any medial gular, the condition tends to be invariant. Species in which the lateral postmentals are only two to three times larger than the medial gulars tend to be variable in this regard and often have the lateral postmentals subequal to the medial gulars or grading into them.

19. SUBLABIALS IN CONTACT WITH INFRALABIALS (Fig. 6). Range: ***0–10.*** In anoles, the first sublabials, when present, are almost always in contact with the first infralabials. If the first sublabial is, as rarely may be the case, separated from the first infralabial by a lateral gular, the coding is, of course, 0,0. Any more posterior sublabials (=abruptly enlarged scales in sequence with the first) may also be in contact with the infralabials, or some or all of them may be separated by a row of smaller scales. If only the first sublabials are in contact with infralabials, or there are no posterior sublabials, the coding is 1,1. In some species, there may be as many as 9 in contact, and the number often differs on the two sides (e.g., 1,2 or 6,7). If there are no sublabials at all the coding is, of course, 0,0.

20. DORSALS (Figs. 7A, B). Flat, smooth: ***1,1.*** *Swollen:* ***2,2.*** *Unicarinate:* ***3,3.*** *Multicarinate:* ***4,4.*** *Triangular or conical crest scales:* ***5,5.*** These conditions should be readily recognizable, but if there is any ambiguity, code a range.

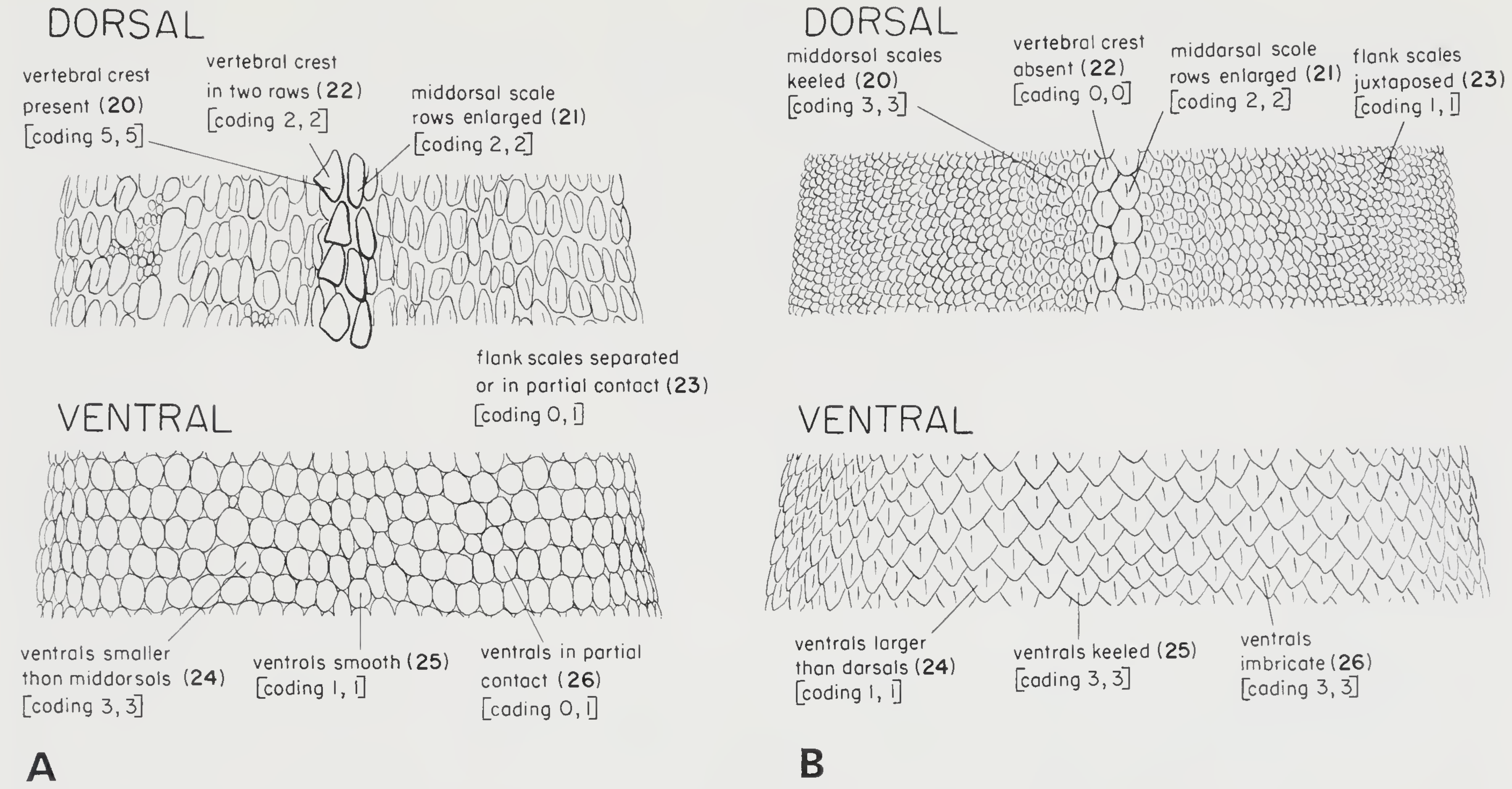
21. ENLARGED MIDDORSAL ROWS (Figs. 7A, B). Range: ***0–30.*** There may be subjectivity in counts of enlarged middorsal rows. In all such cases, code not single numbers but an appropriate range of values. If the enlarged middorsal rows are not countable because of too gradual a transition to the flank scales, code arbitrarily as 30,30.

As in certain other counts, low counts may be more meaningful and repeatable than high counts.

22. MIDDORSAL CRESTS (Fig. 7A). None: ***0,0.*** *Low crest:* ***1,1.*** *High crest:* ***2,2.*** In anoles, "crest" is applied only to one or two rows of sharply enlarged middorsal crests, characteristically triangular or conical, of varying height, but always projecting conspicuously above the paravertebral scales. Most anoles lack such crests.

This is not usually a very useful character. A few anoles have such high crests that I would be remiss if I did not call attention to them.

23. FLANK SCALES (Figs. 7A, B). More or less widely separated: ***0,0.*** *Juxtaposed:* ***1,1.*** *Imbricate:* ***2,2.*** *Heterogeneous:* ***3,3.*** In some, usually giant species, the flank scales are relatively large and may be separated by more or less minute granules. This infrequent condition is coded 0,0. Much more frequently, the flank scales are smaller, and some or all of them are narrowly separated by naked skin or by minute granules, which may allow


DORSAL
vertebral crest present (20) [coding 5, 5]
vertebral crest in two raws (22) [coding 2, 2]
middorsal scale rows enlarged (21) [coding 2, 2]
flank scales separated or in partial contact (23) [coding 0, 1]
VENTRAL
ventrals smaller thon middorsols (24) [coding 3, 3]
ventrols smooth (25) [coding 1, 1]
ventrals in partial contact (26) [cading 0, 1]
A
DORSAL
middorsol scales keeled (20) [coding 3, 3]
vertebral crest absent (22) [cading 0, 0]
middarsal scole rows enlarged (21) [coding 2, 2]
flank scales juxtaposed (23) [coding 1, 1]
VENTRAL
ventrals larger than darsals (24) [coding 1, 1]
ventrals keeled (25) [cading 3, 3]
ventrals imbricate (26) [cading 3, 3]
B

Figures 7A, B. Middorsal scales (above) and ventral scales (below) (characters 20–26).

partial contact. This condition is coded 0,1. Many species have the flank scales juxtaposed; this is coded 1,1. If any of the flank scales clearly overlap, the coding is 2,2. In a few species, the larger scales of the flank may be of very unequal size; these are then scored as heterogeneous: 3,3. The minute granules, which may be present in some cases, are not considered in this definition of heterogeneity.

24. SIZE OF VENTRALS RELATIVE TO DORSALS (Figs. 7A, B). Larger: ***1,1.*** *Equal:* ***2,2.*** *Smaller:* ***3,3.*** *Much smaller:* ***4,4.*** Most anole species have the ventrals larger than the largest dorsals. This may, however, be untrue for species with a distinct zone of enlarged dorsals or those species with crest scales. There may even be noticeable variation in this regard within species. As usual, such variation is coded as a range. The condition—ventrals much smaller than dorsals—is known only in *Chamaeleolis.*

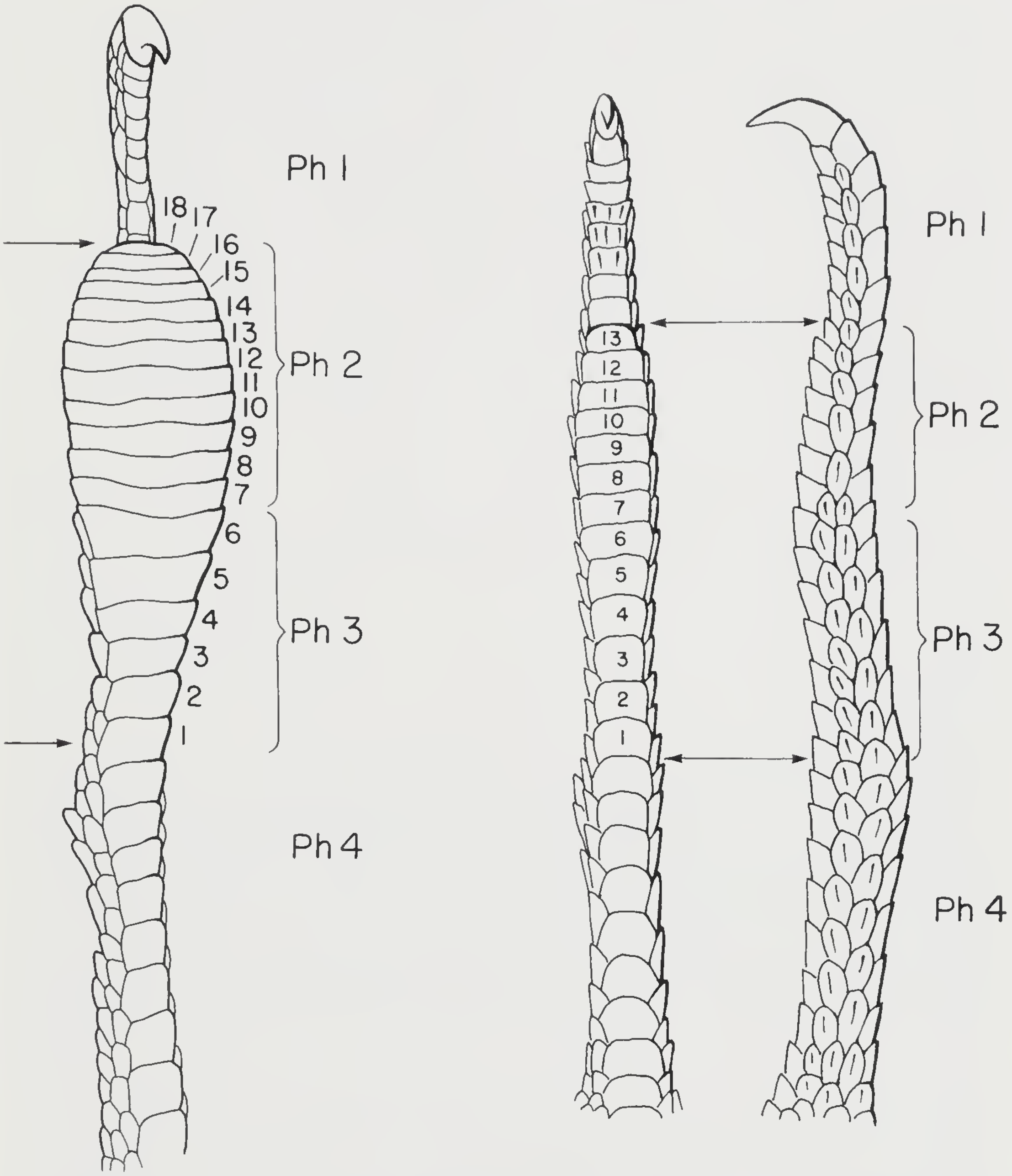
This is often a very useful character.

25. SMOOTH/KEELED VENTRALS (Figs. 7A, B). Smooth: ***1,1.*** *Weakly keeled:* ***2,2.*** *Strongly keeled:* ***3,3.*** Some species are truly variable, with ventrals in some individuals keeled (always unicarinate) and in others smooth. Series from such species should be coded 1,2 or 1,3, as appropriate, and individuals either 1,1, 2,2, or 3,3. Other species have keeling so weak that it is a subjective judgment whether or not it exists at all. Such species may be coded 1,2.

There are just a few species in which ventrals vary from smooth to keeled. In most species this is a strong character.

26. VENTRALS (Figs. 7A, B). Separated: ***0,0.*** *Juxtaposed:* ***1,1.*** *Subimbricate:* ***2,2.*** *Imbricate:* ***3,3.*** Ventrals are sometimes separated by naked skin or granules and often are juxtaposed or subimbricate (intermediate) or distinctly imbricate (distinctly overlapping). More than one condition can occur within a species or even within an individual. In contrast to the last, this is not a strong character, but some species do have strong separation or strong imbrication.

27. TOE PADS (Figs. 8A, B). Pad overlapping first phalanx: ***1,1.*** *Pad not distinct from first phalanx:* ***2,2.*** *No pads:* ***0,0.*** In most species of anoles, the adhesive pad under phalanges ii and iii of all the toes projects distally under the proximal infradigital scales of the first (claw-bearing) phalanx. This is coded 1,1. In a number


Ph I
18
17
16
15
14
13
12
11
10
9
8
7
Ph 2
6
5
4
3
2
1
Ph 3
Ph 4
13
12
11
10
9
8
7
6
5
4
3
2
1
Ph I
Ph 2
Ph 3
Ph 4

Figures 8A, B. Two conditions of the digital pads (characters 27 and 28). Phalanges i–iv are labeled, and appropriate counts of lamellae under the pad are illustrated.

of species, not closely related, the projection is minimal or absent, and the proximal termination of the pad is therefore indistinct (coded 2,2). In the adults of one species only (Fig. 8B), a pad is completely lacking (coded 0,0).

28. LAMELLAR NUMBER (Figs. 8A, B). Range: ***0–50.*** Lamellae are the widened distally overlapping scales characteristic

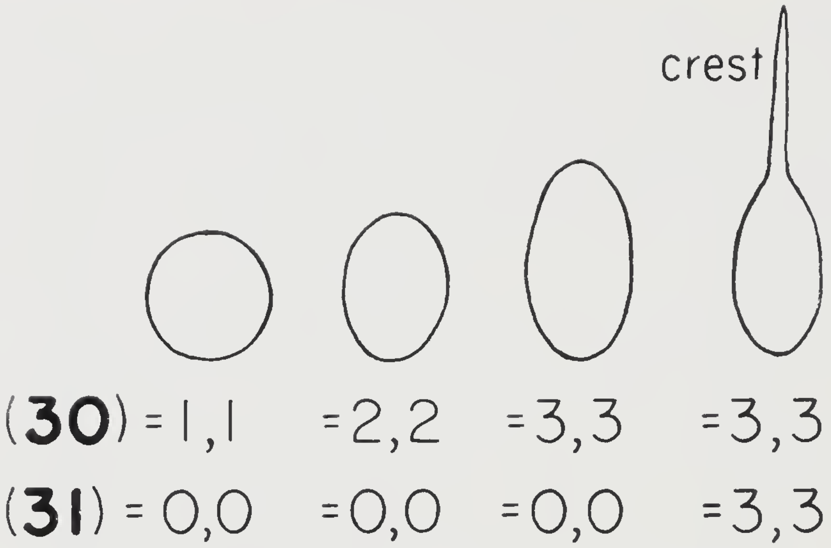


Figure 9. Tail character states (character 30 and 31).

of the adhesive toe pads of anoles. Counts are made only on phalanges ii and iii of the fourth toe of the hind foot. A given range of lamellar counts is species-specific.

Counting lamellar number, as understood here, involves finding the bend between phalanges iii and iv; this is arbitrarily considered the proximal termination of the adhesive pad. A bend also occurs within the pad between phalanges ii and iii, but the distal termination is defined as the joint between phalanges i and ii. Counts are therefore restricted to the lamellae under phalanges ii and iii. At the joint between phalanges iii and iv, the scale at or within the bend is counted. Distally the small terminal lamella of the pad projection is always counted or, in default of such a scale, the scale that lies across the joint between phalanges i and ii.

The intention here is to count only scales of the pad proper. For most anole species, the procedure outlined above probably closely approximates reality. However, scanning electron microscopy has revealed that, in fact, the adhesive lamellae with the functionally adhesive hairs are not necessarily confined within the boundaries of phalanges ii and iii. However, these boundaries provide a convenient macrostructural definition on which to base reproducible counts. Ultimately, however, the justification for this count, rather than counts of all lamellae under the fourth toe, is historical: Boulenger (1885), who first provided standard and recognizable descriptions of anole species, used the count of la-

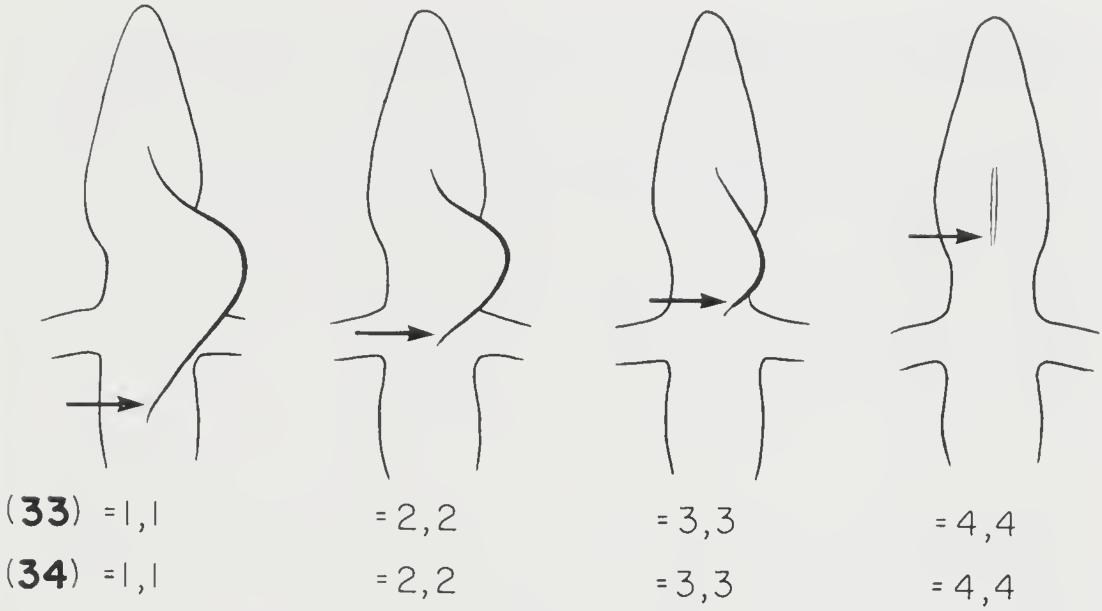


Figure 10. Dewlap extent (characters 33 and 34). Arrow points to posterior termination of dewlap.

mellae under phalanges ii and iii. Stejneger, Cochran, Schwartz, and Williams have routinely used this count.

It is a source of some confusion that workers on Mexican and Central American anoles have rather consistently used other counts, especially the total number of subdigitals under the fourth hind toe. The attempt here is to standardize lamellar counts with those conventionally used for West Indian and South American anoles.

29. SUPRADIGITALS. Smooth: ***1,1.*** *With indistinct or single keels:* ***2,2.*** *Multicarinate:* ***3,3.*** Most anoles have multicarinate supradigital scales. The alternative conditions—smooth (1,1) or with indistinct, usually single keels (2,2)—are relatively uncommon and, therefore, when they do occur, diagnostic.

30. TAIL (Fig. 9). Round: ***1,1.*** *Weakly compressed:* ***2,2.*** *Strongly compressed:* ***3,3.*** Strongly compressed tails are readily recognized. Weakly compressed or round tails are common.

31. TAIL CREST (Fig. 9). None: ***0,0.*** *Serrate:* ***1,1.*** *Distinct crest:* ***2,2.*** *High crest:* ***3,3.*** Round tails have no crests. Weakly compressed tails may or may not be serrate above. Strongly compressed tails may or may not have a crest, and may not even be serrate above, and, if present, the crest may be high or low. Females rarely have high crests and variation from population to population within a species and within a sex is not unusual.

32. POSTANALS. Present: ***1,1.*** *Obscure:* ***2,2.*** *Absent:* ***3,3.*** The characteristic enlarged postanal scales of male anoles are usually laterally expanded ovals, somewhat resembling airplane propellers, a variable distance behind the vent. They may also be round, large or small, obscure, or, as in males of not a few species, and always in females, absent.

33. DEWLAP (Male) (Fig. 10). Large: ***1,1.*** *Intermediate:* ***2,2.*** *Small:* ***3,3.*** *Absent:* ***4,4.*** Dewlaps should be scored as large if they extend onto the belly past the insertion of the arms, intermediate if they reach just the level of the axilla, and small if they are shorter than this. If the animal is female, code 888,888 in the IBM version, or NA in the Macintosh version.

Large (1,1), as defined here, is a very inclusive term, and species so coded will differ conspicuously in the dewlap area. The present definition has been adopted to avoid the problem of quantifying dewlap area and to permit the scoring of dewlaps that are not extended in preserved animals.

34. DEWLAP (Female) (Fig. 10). Large: ***1,1.*** *Intermediate:* ***2,2.*** *Small:* ***3,3.*** *Absent:* ***4,4.*** Females may possess a dewlap, which is then scored just as in males. However, both an indication—a mere zone of differentiated scales—or a mere fold (i.e., any structure that could not be substantially extended) and a complete absence should be scored 4,4. If the animal examined is a male, code 888,888 in the IBM version, or NA in the Macintosh version.

35. SNOUT–VENT MAXIMUM (Male). Range: ***0–300.*** Snout–vent length should be measured on every specimen. The number with which this length is compared in the coded matrix is the maximum known for the relevant sex in each species. Only if the matrix number is exceeded by a substantial margin should a tentative identification be rejected.

A 0 is used as the minimum for size only because hatchling size is unknown for most anoles.

A female should be coded 888,888 in the IBM version, or NA in the Macintosh version.

36. SNOUT–VENT MAXIMUM (Female). Range: ***0–300.*** The principles suggested for the interpretation of the comparable entry in males apply here also. For a male, code this entry 888,888 in the IBM version, or NA in the Macintosh version. As in males, 0 is treated as the minimum only because hatchling size is nearly unknown or unreported in anoles.

37. TAIL LENGTH/BODY LENGTH. Ratios between 0.8 and 1.2: ***1,1.*** *Ratios between 1.3 and 1.7:* ***2,2.*** *Ratios between 1.8 and 2.2:* ***3,3.*** *Ratios between 2.3 and 2.7:* ***4,4.*** *Ratios between 2.8 and 3 or more:* ***5,5.*** Tail length should be measured whenever the tail is neither broken nor regenerated. (The regenerated portion of a lizard tail always differs in scale form from the unregenerated portion; such difference in scale form is never seen in an unregenerated tail.)

The measured tail length must then be compared with the snout–vent length, and the ratio of tail length over body (snout–vent) length obtained. Ratios between 0.8 and 1.2 should be coded 1,1. Ratios between 1.3 and 1.7 may be coded 2,2; those between 1.8 and 2.2 coded 3,3; those between 2.3 and 2.7 coded 4,4; and those between 2.8 and 3 or more 5,5. All intermediates should be so coded (e.g., individuals with ratios 2.75 as 4.5; series with ratios ranging from 1.5 to 1.9 as 2,3).

V. ANOLEKEY—OPERATIONAL INSTRUCTIONS

Ernest E. Williams

The ANOLEKEY is menu-driven and is available in two versions, one in Basic for the IBM PC, written by Hugh and Stanley Rand, and one in HyperCard for the Macintosh, written by Robert O'Hara. Both versions do essentially the same job but differ in one aspect. The HyperCard version for the Macintosh is essentially a database for all anoles with an ANOLEKEY as one of the options and the reference matrices as part of the database.

At this time, most reference matrices are not finished and lack the added feature of descriptors. Only Puerto Rico, Jamaica, Ecuador, and Costa Rica–Panama subsets of the total database are available at this time. However, it is hoped to add other subsets in the near future.

Because the ANOLEKEY itself is functional, and we welcome suggestions and improvements, we have decided to go public at this time. A copy of ANOLEKEY and associated documentation (Hugh and Stanley Rand, 1994, for the IBM PC, and Robert

O'Hara and Ernest Williams, 1994, for the Macintosh) is available to anyone interested in trying the ANOLEKEY and willing to report bugs and/or suggest improvements. Each copy will include a description of the 37 characters and how to count them (Williams, this paper). (For the IBM version, write to A. S. Rand [include formatted disk]; for the Macintosh version, write to E. E. Williams [include formatted disk].)

In addition to the ANOLEKEY and its documentation, the distribution disk for the IBM includes a version of the Basic Program that is not customized for use with the anoles but that can be used with any group. For a comparable bare-bones HyperCard for the Macintosh version, write to E. E. Williams.

VI. ANOLEKEY IN BASIC FOR THE IBM PC

A. Stanley Rand

The IBM version of ANOLEKEY consists of a Basic Program, a "Readme" file that describes the use of the program, a text file describing the 37 anole characters, and several reference matrices, all stored on a single floppy disk. The program was created in MS-DOS, is stored in ASCII, and may be loaded and run using BASICA, Turbo BASIC, or Quick Basic. The program should run on any IBM PC or clone.

The disk contains two versions of the program adapted to identify anoles, one that prints out a hard copy of results and the other that does not. There is also a stripped down version that lacks the modifications for use with anoles so that it can be used for any group.

The reference matrices each contain information on all the recognized species of anoles from a specific geographic area. Four areas are currently available: Puerto Rico, Jamaica, Panama–Costa Rica, and Ecuador. Each matrix contains the ranges for the 37 standard characters for each species and the short list of diagnostic characteristics, the "descriptor," for each species.

The program allows you to load a reference matrix (e.g., Panama–Costa Rica) and then enter the information for the 37 standard characters for an individual or series to be identified. Most of these characters are scale characters, two involve size, and one involves proportions. A list of these characters and their codings is given in Appendix 2 of the "Readme" file. Some of these characters are counts that are entered directly; the others must be coded. You are prompted for each character and informed of the possible codings. For each character, the program will accept only an appropriate range of values. You must enter for each character two numbers separated by a comma, a minimum and a maximum. This allows you to enter information from a series of animals, to code the two sides of an animal if they are different, and to code an ambiguous situation. The data for the unknown can be corrected and stored in a file.

Once the data are entered and checked, the program asks you to enter the number of characters where a species in the reference matrix with which the unknown is being compared must differ before being eliminated as a possible match. The larger this number, the more species are matched and the more different they may be from the unknown.

The program then compares the unknown with the reference matrix and produces a report that lists the species that match, giving for each the total number of characters in which it differs, what the differing characters are, and how great the differences, positive or negative, are. For each matching species the program supplies a short description of characters such as color, distribution, and any peculiarities that could help in identification.

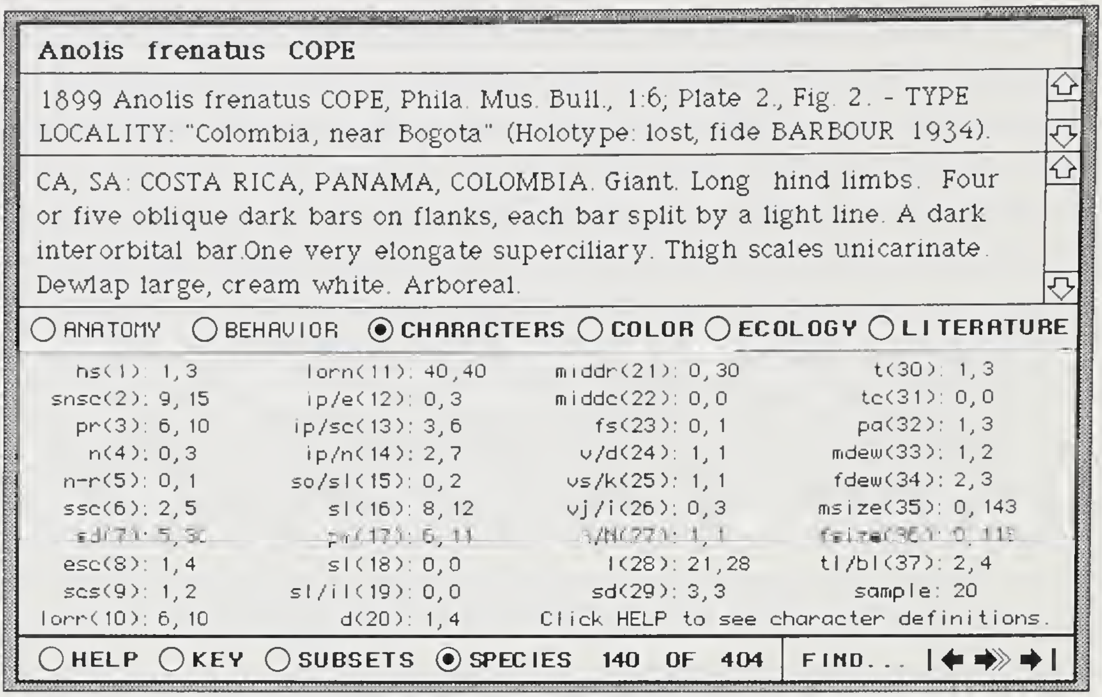
The program allows you to create or change a reference matrix, although creating a reference matrix is probably more easily done with a word-processing program outside of ANOLEKEY. The details of the format for a reference matrix are given in the "Readme" file.

As a shortcut, there is also the option of comparing an unknown with the reference matrix using only two characters, instead of all 37. This will be useful if the unknown has among its 37 standard characters one or two states that are so rare or unusual that only one, two, or at most three species can possibly be matches. The descriptor or descriptors will confirm the identification.

VII. THE *ANOLIS HANDLIST:* A HYPERCARD VERSION OF THE ANOLEKEY

Robert J. O'Hara and Ernest E. Williams

The Macintosh version of the ANOLEKEY is much more than a computer key, and to better indicate its multiple functions we



Anolis frenatus COPE

1899 Anolis frenatus COPE, Phila. Mus. Bull., 1:6; Plate 2., Fig. 2. - TYPE LOCALITY: "Colombia, near Bogota" (Holotype: lost, fide BARBOUR 1934).

CA, SA: COSTA RICA, PANAMA, COLOMBIA. Giant. Long hind limbs. Four or five oblique dark bars on flanks, each bar split by a light line. A dark interorbital bar.One very elongate superciliary. Thigh scales unicarinate. Dewlap large, cream white. Arboreal.

○ ANATOMY ○ BEHAVIOR ● CHARACTERS ○ COLOR ○ ECOLOGY ○ LITERATURE

```
     hs(1): 1,3        lorn(11): 40,40    middr(21): 0,30        t(30): 1,3
  snsc(2): 9, 15       ip/e(12): 0,3      middc(22): 0,0        tc(31): 0,0
    pr(3): 6, 10      ip/sc(13): 3,6         fs(23): 0, 1       pa(32): 1,3
     n(4): 0,3         ip/n(14): 2,7        v/d(24): 1, 1     mdew(33): 1,2
   n-r(5): 0, 1       so/sl(15): 0,2       vs/k(25): 1, 1     fdew(34): 2,3
   ssc(6): 2,5           sl(16): 8, 12     vj/i(26): 0,3     msize(35): 0, 143
    sd(7): 5, 30         pr(17): 6, 11      s/N(27): 1, 1    fsize(36): 0, 115
   esc(8): 1,4           sl(18): 0,0          l(28): 21,28    tl/bl(37): 2,4
   scs(9): 1,2        sl/il(19): 0,0         sd(29): 3,3        sample: 20
 lorr(10): 6, 10          d(20): 1,4     Click HELP to see character definitions.
```

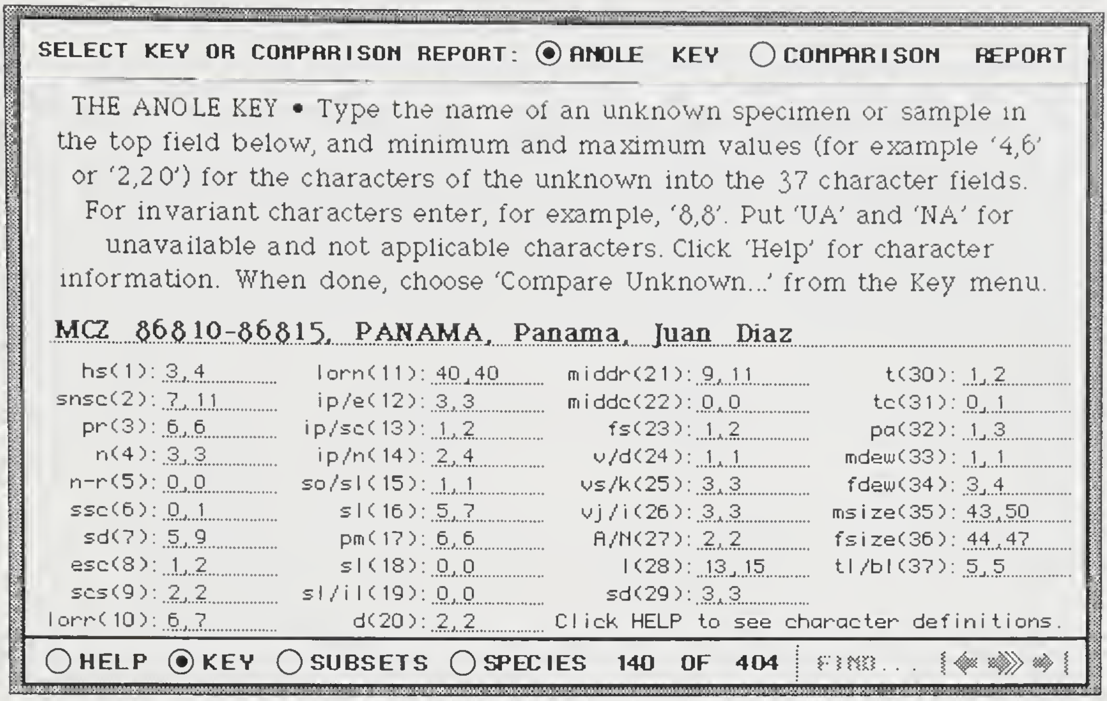
○ HELP ○ KEY ○ SUBSETS ● SPECIES 140 OF 404 FIND...

Figure 11. Species card for *Anolis frenatus* from the *Anolis Handlist.* The buttons at the lower left, present on every card in the stack, allow the user to choose the Help, Key, Subset Editor, or Species cards. The diagnostic characters are now being shown on this card; information on anatomy, behavior, color, ecology, or literature may be displayed by clicking on the appropriate button.

refer to it as the *Anolis Handlist.* In addition to serving as a key, the *Anolis Handlist,* when completed, is intended to be an index and checklist for the possibly more than 400 species of *Anolis, Chamaeleolis, Chamaelinorops,* and *Phenacosaurus* residing in North, Central, and South America.

Although the *Anolis Handlist* is still incomplete, as already mentioned, we describe it here as though it were complete. While waiting for EEW to complete additional reference matrices along with the several subsidiary COLOR, etc., fields, described below, the ANOLEKEY is fully functional.

The *Anolis Handlist* was created with Apple Computer's HyperCard, an object-oriented software development environment that makes use of all of the standard elements of the Macintosh interface, including pull-down menus, windows, buttons, and scroll bars (Apple Computer, 1987). HyperCard documents may be thought of as groups of interactive electronic file cards:



SELECT KEY OR COMPARISON REPORT: ● ANOLE KEY ○ COMPARISON REPORT

THE ANOLE KEY • Type the name of an unknown specimen or sample in the top field below, and minimum and maximum values (for example '4,6' or '2,20') for the characters of the unknown into the 37 character fields. For invariant characters enter, for example, '8,8'. Put 'UA' and 'NA' for unavailable and not applicable characters. Click 'Help' for character information. When done, choose 'Compare Unknown...' from the Key menu.

MCZ 86810-86815, PANAMA, Panama, Juan Diaz

hs(1): 3,4
snsc(2): 7,11
pr(3): 6,6
n(4): 3,3
n-r(5): 0,0
ssc(6): 0,1
sd(7): 5,9
esc(8): 1,2
scs(9): 2,2
lorr(10): 6,7
lorn(11): 40,40
ip/e(12): 3,3
ip/sc(13): 1,2
ip/n(14): 2,4
so/sl(15): 1,1
sl(16): 5,7
pm(17): 6,6
sl(18): 0,0
sl/il(19): 0,0
d(20): 2,2
middr(21): 9,11
middc(22): 0,0
fs(23): 1,2
v/d(24): 1,1
vs/k(25): 3,3
vj/i(26): 3,3
A/N(27): 2,2
l(28): 13,15
sd(29): 3,3
t(30): 1,2
tc(31): 0,1
pa(32): 1,3
mdew(33): 1,1
fdew(34): 3,4
msize(35): 43,50
fsize(36): 44,47
tl/bl(37): 5,5

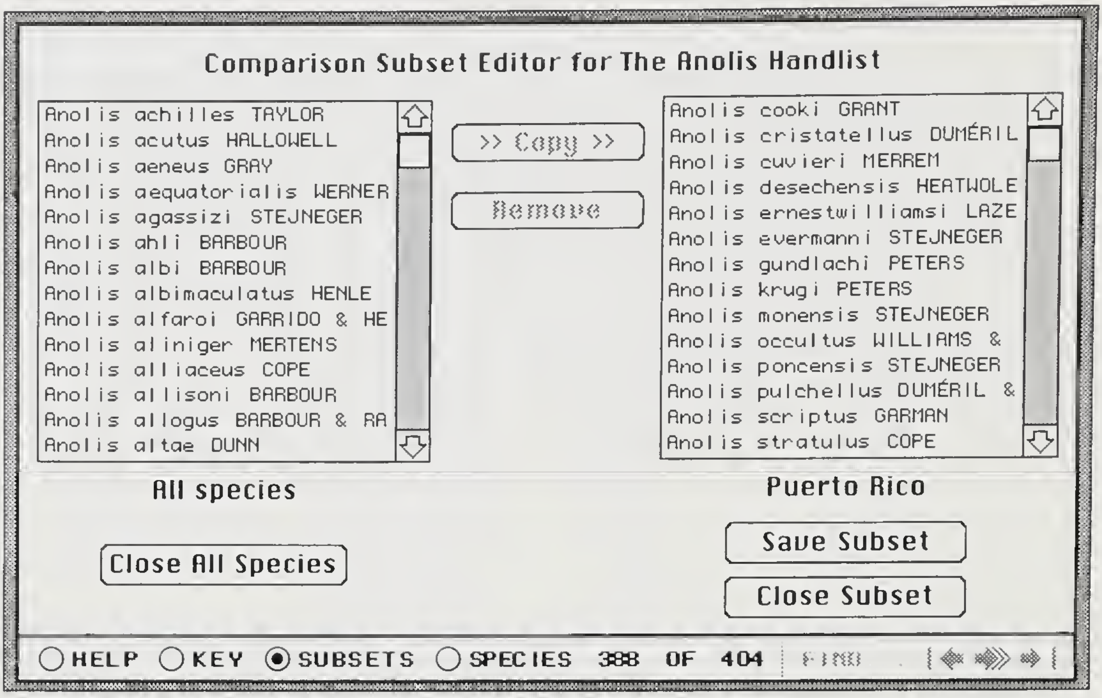
Click HELP to see character definitions.

○ HELP ● KEY ○ SUBSETS ○ SPECIES 140 OF 404

Figure 12. The Key card, with data from a series to be compared entered into the character fields.

each HyperCard document is known as a "stack," and each stack is made up of one or more individual screens, or "cards" (Apple Computer, 1989). The *Anolis Handlist* is a single HyperCard stack, and it consists of more than 400 Species cards (some of the species are undescribed or not well understood), a Key card, a Subset Editor card for use with the Key, and a Help card that provides general information as well as definitions of diagnostic characters (see Section V, earlier).

Each Species card displays in the upper two fields the name, author, original citation, and type locality and in the bottom two fields two kinds of characters: (1) the "descriptors," those that are especially diagnostic, i.e., special for individual species, and (2) the characters that are routinely recorded for all species (Fig. 11). Also on each Species card, provision is made for information on anatomy, behavior, color, ecology, and literature, and this information may be recorded and read on fields called up by choosing the corresponding button the middle row between the upper and lower fields. The Species cards may be browsed one by one using the navigational buttons in the lower right corner


Comparison Subset Editor for The Anolis Handlist
>> Copy >>
Remove
All species
Puerto Rico
Close All Species
Save Subset
Close Subset
○ HELP ○ KEY ● SUBSETS ○ SPECIES 388 OF 404
FIND

Anolis achilles TAYLOR
Anolis acutus HALLOWELL
Anolis aeneus GRAY
Anolis aequatorialis WERNER
Anolis agassizi STEJNEGER
Anolis ahli BARBOUR
Anolis albi BARBOUR
Anolis albimaculatus HENLE
Anolis alfaroi GARRIDO & HE
Anolis aliniger MERTENS
Anolis alliaceus COPE
Anolis allisoni BARBOUR
Anolis allogus BARBOUR & RA
Anolis altae DUNN

Anolis cooki GRANT
Anolis cristatellus DUMÉRIL
Anolis cuvieri MERREM
Anolis desechensis HEATWOLE
Anolis ernestwilliamsi LAZE
Anolis evermanni STEJNEGER
Anolis gundlachi PETERS
Anolis krugi PETERS
Anolis monensis STEJNEGER
Anolis occultus WILLIAMS &
Anolis poncensis STEJNEGER
Anolis pulchellus DUMÉRIL &
Anolis scriptus GARMAN
Anolis stratulus COPE

Figure 13. The Subset Editor card. The scrolling field on the left lists all the species in the *Anolis Handlist,* and the field on the right contains one of the comparison subsets. These subsets may be edited and saved for future use with the Key.

of the cards, and they may be sorted according to species name, year of description, or any chosen diagnostic character by making the appropriate selection from a pull-down menu. Species cards may be added, deleted, or edited at the discretion of the user. Every scrolling field on each Species card can hold up to 30,000 text characters; thus, the field for original citation could in fact contain a full synonymy, or the literature field an extensive bibliography. All the data in the Species cards may be searched at will by selecting the FIND button (Fig. 11).

The Key card (Fig. 12) permits the user to enter values for the diagnostic characters of an unknown specimen or series and to compare this unknown to all the Species cards or to a subset of the Species cards. When going to the Key card from a Species card, the option is provided to automatically read the data from that Species card into the Key as if it were an unknown, thus permitting comparisons among known species as well as among unknowns and knowns. Once the characters of a specimen or species to be compared have been entered on the Key card, the user selects "Compare Unknown" from a pull-down menu and responds to a series of prompts asking, for example, by how much the unknown may differ from the reference data on the Species cards and still be considered a match.

The Subset Editor (Fig. 13) is an adjunct to the Key card. Comparison of an unknown to all of the Species cards in the

A report from The Anolis Handlist by E. E. Williams

Sunday, April 10, 1994, 4:48 PM

```
''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' compared with the
subset ''PANAMA.''

• Anolis auratus DAUDIN
  CA, SA: eastern and central PANAMA, COLOMBIA, ECUADOR, VENEZUELA,
  BRAZIL. Small. Toepads not overlapping first phalanx. Light lat-
  eral line. Dewlap large, blue or black. Sharply enlarged keeled
  middorsals. In grass.
    ''MCZ 86810-86815, PANAMA, Panama, Juna Diaz'' misses by 0 out
  of 37 key characters.
• Anolis biporcatus (WIEGMANN)
  CA, SA: MEXICO, GUATEMALA, EL SALVADOR, NICARAGUA, COSTA RICA,
  PANAMA, COLOMBIA. Large. Heavy bodied. Green changing to dark
  brown. Dewlap moderate in male, white basally, mostly powder blue
  with red-orange free margin, in female smaller, sometimes with
  black flecks. In canopy.
    ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out
  of 37 key characters:
      n(4) by 1, n-r(5) by -1, A/N(27) by 1, l(28) by -1, tl/bl(37) by
      1
• Anolis humilis PETERS
  CA: NICARAGUA, COSTA RICA, PANAMA. Small, Brown. Dewlap large, red
  with bright yellow margin. Axillary pits. About 10 middorsal rows
  enlarged, larger than ventrals, the two median rows smallest. On
  or near ground.
    ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out
  of 37 key characters:
      lorn(11) by 1, d(20) by -1, v/d(24) by -2, A/N(27) by 1, tl/
      bl(37) by 3

• Anolis intermedius PETERS
  CA: COSTA RICA, PANAMA. Small, Brown or greyish. Dewlap bone white.
  Arboreal.
```

''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 4 out of 37 key characters:

lorn(11) by 13, so/sl(15) by 1, A/N(27) by 1, tl/bl(37) by 2

- Anolis kemptoni DUNN
  CA: PANAMA. Small. Greyish brown. White line under the eye. Dewlap skin red with orange anterior spot, scales whitish. Arboreal.
  ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 3 out of 37 key characters:
  so/sl(15) by 1, A/N(27) by 1, tl/bl(37) by 2

- Anolis lemurinus COPE
  CA: MEXICO, GUATEMALA, HONDURAS, NICARAGUA, COSTA RICA, PANAMA. Moderate size. Olive brown with dark dorsal blotches or (females diamond-shaped middorsal markings or a black-edged middorsal stripe. Dewlap dark red with black scales. In Panama only in western and central regions.
  ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out of 37 key characters:
  n(4) by 1, d(20) by -1, A/N(27) by 1, l(28) by -1, tl/bl(37) by 2

- Anolis lionotus COPE
  CA: PANAMA. Moderate size. Light lateral line. A dorsal zone of about 10 rows of enlarged smooth scales much larger than ventrals. Dewlap large, orange. Semiaquatic. Only central Panama.
  ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out of 37 key characters:
  n(4) by 1, d(20) by 1, v/d(24) by -2, A/N(27) by 1, tl/bl(37) by 2

- Anolis poecilopus COPE
  CA, SA: PANAMA, COLOMBIA. Moderate size. Light lateral line. Dewlap large, orange. Head scales small. A dorsal zone of about 20 rows of enlarged keeled scales about as large as ventrals. Semiaquatic. In Panama only in eastern region, in Colombia only in western region.
  ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 4 out of 37 key characters:
  snsc(2) by -3, n(4) by 1, A/N(27) by 1, tl/bl(37) by 2

- Anolis tropidogaster HALLOWELL
  CA, SA: PANAMA, COLOMBIA. Small. Often an indication of a light middorsal stripe in both sexes. Dewlap yellow, orange or reddish. Trees and bushes.

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  ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out
of 37 key characters:
   n(4) by 2, ssc(6) by -1, d(20) by -1, A/N(27) by 1, tl/bl(37) by
   2

• Anolis vittigerus COPE
  CA, SA: PANAMA, COLOMBIA. Moderate size. Variable and complex pat-
  tern on nape. Dewlap with central dark spot. In Panama only in east-
  ern region.
   ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 5 out
  of 37 key characters:
     middr(21) by -1, A/N(27) by 1, l(28) by -1, mdew(33) by -1, tl/
     bl(37) by 1

• Anolis woodi DUNN
  CA: COSTA RICA, PANAMA, Cordillera Talamanca. Large. Olive with
  indistinct rusty spots. Dewlap pink orange at edge, amber yellow
  in middle, bluish white at base.
   ''MCZ 86810-86815, PANAMA, Panama, Juan Diaz'' misses by 4 out
  of 37 key characters:
     n(4) by 1, ip/e(12) by 2, A/N(27) by 1, tl/bl(37) by 1
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Figure 14. A Comparison Report from the *Anolis Handlist.* Reports may be edited and printed with the standard HyperCard facilities or copied into any word processor for editing and printing.

Anolis Handlist may be time-consuming, and in most cases some additional information about the unknown (such as its collecting locality) or its species group will permit a comparison to be restricted to some subset of the total collection of species. The Subset Editor allows the user to assemble comparison subsets, either manually or automatically, to save these subsets for future use and to edit them as necessary. When making a comparison with the Key, the user may specify that the comparison be made against one of the existing subsets.

The result of a comparison made with the Key is a Comparison Report (Fig. 14). This report specifies the name of the unknown that was compared, the name of the subset (if any) to which it was compared, the number of characters that differ between the unknowns and the knowns, and by how much these characters differ. The Comparison Report may be printed using the PRINT

FIELD option under FILE. (PRINT CARD will print only the portion of any field visible initially.)

The *Anolis Handlist* has been designed specifically for the Macintosh computer. The principles it embodies are general ones, however, and these principles could be implemented on a variety of computer platforms.

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We acknowledge with special gratitude the struggles of two anonymous reviewers to catch errors, typographical and other, revise the logic of our discussions, and, with all good will, to generally emend and improve our paper. Nancy Knowlton and John Cadle saw a much later version. We also greatly appreciate their helpful comments.

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CYEMATID LARVAE OF THE *LEPTOCEPHALUS HOLTI* GROUP IN THE ATLANTIC AND PACIFIC OCEANS (PISCES: SACCOPHARYNGIFORMES)

DAVID G. SMITH[1] AND MICHAEL J. MILLER[2]

ABSTRACT. Cyematid larvae of the *Leptocephalus holti* group consist of three distinct species or species groups, each found in the Atlantic and Pacific oceans. Species 1 has four gut loops and lacks pigment along the lateral midline. Species 2 also has four gut loops, but it has lateral pigment. Species 3 has three gut loops and lacks lateral pigment. The name *Leptocephalus holti* is used as a convenient group name to refer to a complex of related species, none of which has been conclusively identified with an adult. Larvae of the *Leptocephalus holti* group may belong to *Neocyema* Castle, but this identification cannot yet be confirmed.

INTRODUCTION

The family Cyematidae is among the strangest and most highly modified of the deep-sea eels. Only the gulpers (Saccopharyngidae, Eurypharyngidae, and Monognathidae) exceed it in the degree of skeletal reduction. For nearly a century, the family was known from a single species, *Cyema atrum* Günther, 1878, found in all oceans at depths of 1,500–3,000 m (Bertin, 1937:25). Castle (1977) described a second genus and species, *Neocyema erythrosoma,* from two specimens collected in the South Atlantic Ocean. Evidence of a second cyematid species, however, had existed long before Castle's discovery in the form of an unidentified leptocephalus. The leptocephalus of *Cyema atrum* was first collected by the *Michael Sars* North Atlantic Expedition in 1910 and illustrated (but not named) by Murray and Hjort (1912, fig. 79). It was identified as *Cyema atrum* by Lea (1913:19), largely on the

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basis of the unusually low number of myomeres, and confirmed by Roule and Bertin (1929:108) through the discovery of metamorphic specimens. Even before this, however, Schmidt (1909: 6) described *Leptocephalus holti* from material collected by the Danish vessel *Thor* in the northeastern Atlantic. He made no attempt to identify it beyond speculating that it and some other leptocephali might represent "southern warm-water forms which have been taken at their northern limits in the 'Thor's' investigation." Larvae of the *L. holti* type were not reported again until Raju (1974:559) found a similar specimen in the South Pacific. Raju pointed out its resemblances to the larva of *Cyema atrum* and felt "compelled to relate it to an unknown species of the Cyemidae [sic]." Tabeta (1988:29) described two *L. holti*–like forms as "Cyematidae sp. 1" and "Cyematidae sp. 2"; species 1 differed from species 2 and from Schmidt's and Raju's specimens in lacking the conspicuous midlateral pigment spots. Fortuño and Olivar (1986; also Olivar and Fortuño, 1991) reported a specimen collected in the South Atlantic off Namibia. They noted that their specimen lacked lateral pigment and speculated that this character might appear later in development. Smith (1989b:945) reported three additional specimens from the Sargasso Sea and the equatorial Atlantic and agreed with Raju that they probably belonged to the Cyematidae. Smith's specimens also lacked midlateral pigment spots, and they had slightly fewer myomeres than Schmidt's holotype of *L. holti.* Based on the limited material available, he was unable to assess the significance of these differences.

In this paper, we report on 47 additional specimens from both the Atlantic and Pacific oceans. These have revealed previously unsuspected diversity in several characters and allow us to give a more complete account of these distinctive larvae than has heretofore been possible.

MATERIAL AND METHODS

Most of our material (30 specimens) was collected during five cruises in the subtropical convergence zone of the Sargasso Sea between 1981 and 1989 (Kleckner *et al.,* 1983; Kleckner and McCleave, 1988; Miller, 1993). These cruises were designed to study the spawning and larval distribution of the eel *Anguilla rostrata.* The other new Atlantic specimen was collected near

Bermuda. Including the five previously recorded specimens (Schmidt, 1909; Fortuño and Olivar, 1986; Smith, 1989b), the total number of specimens known from the Atlantic is now 36. Of the 16 new Pacific specimens, 4 were found in collections at the Natural History Museum of Los Angeles County, 9 at Scripps Institution of Oceanography, and 3 at the National Marine Fisheries Service Honolulu laboratory. With the nine previously recorded specimens (Raju, 1974; Tabeta, 1988), 25 specimens are now know from the Pacific. Specimens examined are deposited in the Academy of Natural Sciences of Philadelphia (ANSP); Museum of Comparative Zoology, Harvard University (MCZ); Natural History Museum of Los Angeles County (LACM); National Museum of Natural History, Washington, D.C. (USNM); and Scripps Institution of Oceanography, La Jolla, California (SIO).

Counts and measurements follow the methods of Smith (1989a: 665). Near the tip of the tail, myomeres become difficult to count, and in most cases only approximate counts were possible. The small size of most of our specimens made it difficult to obtain precise numerical values for any of the characters. The position of the last vertical blood vessel (LVBV) could not be seen clearly at the point where it entered the dorsal aorta in any of the specimens. We estimate this point to be on the average some six to eight myomeres anterior to a vertical line through the anus. Numbers in parentheses following meristic values represent the number of specimens on which the count is based.

We use the term "*Leptocephalus holti*" in the sense of Orton (1964a;199, 1964b:438) as a convenient group name to refer to what is apparently a complex of closely related species. In referring to the three distinct types (whether each represents a single species or a complex within the larger *holti* complex), we follow Tabeta (1988) in calling them species 1, species 2, and (newly described here) species 3.

GENERAL DESCRIPTION OF *LEPTOCEPHALUS HOLTI* (AFTER SMITH, 1989b:946)

Body moderately deep, depth about one-sixth to one-third standard length (SL); body deepens gradually behind head. Gut with a distinct swelling at hepatogastric region and two or three loops or arches behind this; a compact liver lobe near 17th myomere,

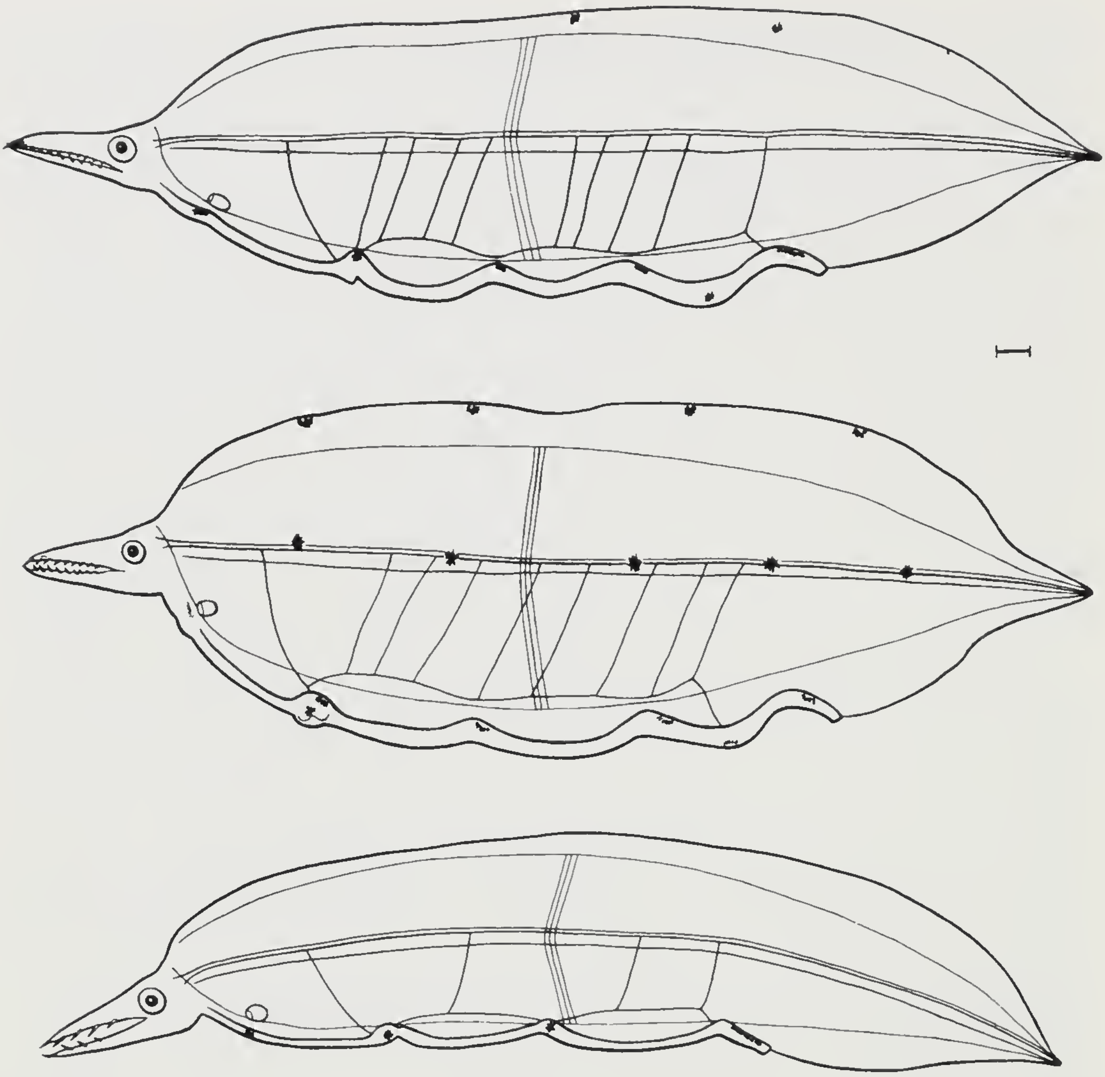

Figure 1. The *Leptocephalus holti* group. Top, species 1, MCZ 101007, 30 mm SL; Middle, species 2, MCZ 101003, 26 mm SL; Bottom, species 3, MCZ 101023, 25 mm SL. Drawn by L. Meszoly.

contributing to swelling of gut; pancreas compact, located just posterior to liver and gall bladder; dorsal aorta sending several conspicuous vertical blood vessels that enter a parallel ventral vessel that lies distinctly above the gut. Dorsal fin begins approximately 20 myomeres anterior to anus. Head and snout long; eye located posteriorly, close to anteriormost myomeres; snout long and pointed, profile relatively flat; nasal capsule small. Several expanded melanophores sometimes present on lateral midline. Moderately large melanophores on gut. One to four melanophores sometimes present near dorsal margin of body, in clear area above myomeres. Pigment usually present at anterior tip of

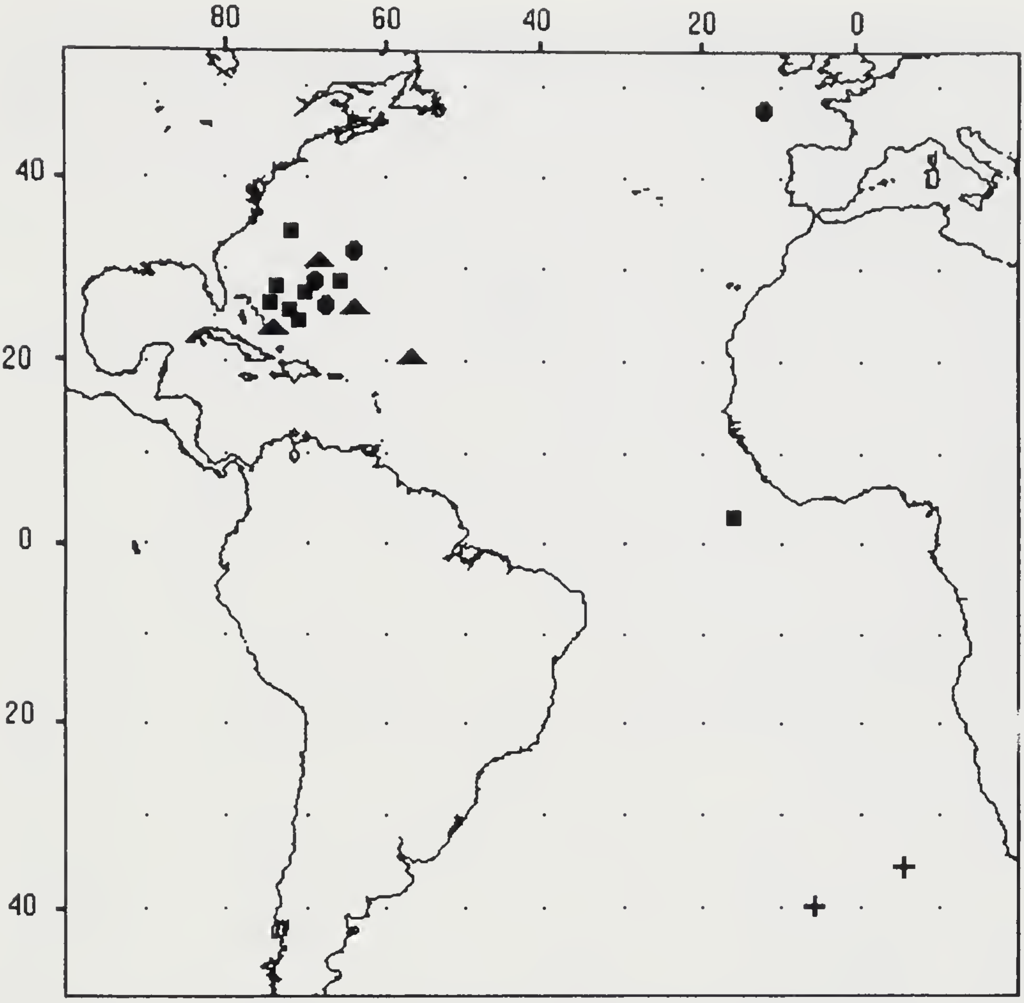

Figure 2. Distribution of *Leptocephalus holti* and *Neocyema erythrosoma* in the Atlantic. Square = species 1; circle = species 2; triangle = species 3; cross = *Neocyema erythrosoma.*

snout and lower jaw. Maximum size unknown, though probably not large. Largest specimen known 43 mm SL; all specimens premetamorphic.

Species 1
Figures 1 (top), 2, 3

Diagnosis. Four gut loops, including hepatogastric swelling. No pigment on side of body along lateral midline. One to three melanophores near dorsal margin of body above myomeres. Paired melanophores laterally on gut adjacent to pectoral fin and posteriorly between third and fourth gut loops; a single or complex melanophore dorsal to each gut loop. Pigment at tip of snout and

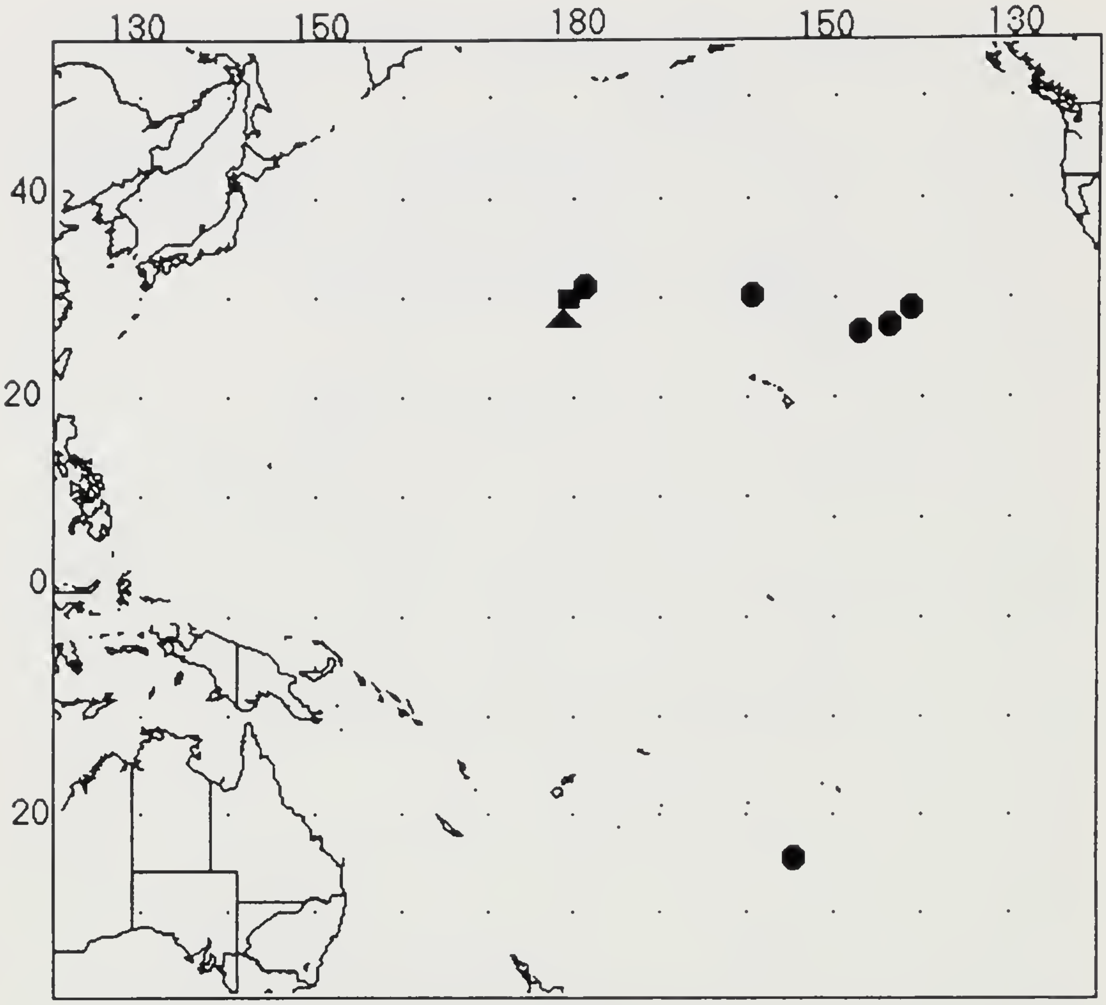

Figure 3. Distribution of *Leptocephalus holti* in the Pacific. *Square* = species 1; circle = species 2; triangle = species 3.

lower jaw. Myomeres: total ca. 99–117 (15 specimens), preanal 45–65 (20).

Size. Ca. 10–39 mm SL, all premetamorphic.

Variation. All but two of the Atlantic specimens came from the Sargasso Sea, the others from off the west coast of Africa (Fig. 2). The latter had approximately 99–105 total myomeres compared to ca. 108–117 for the western Atlantic specimens. There seem to be no other differences between the eastern Atlantic and western Atlantic specimens. Tabeta (1988:29) gave a range of 97–100 total, 51–62 preanal, and 46–49 LVBV myomeres for his seven western Pacific specimens, 16–31 mm in length. The single central Pacific specimen examined, USNM 324871, had significantly fewer preanal myomeres (ca. 45) than either the Atlantic specimens (ca. 49–65) or the western Pacific specimens (51–62).

Material Examined. Atlantic (25, ca. 9–39 mm SL): MCZ 64484 (1, 31), 34°27.0′N, 71°18.5′W, 250–0 m, 13 Apr 1977. 65647 (1, 20), 4°05.2′N, 17°20.8′W, 75 m, 15 Nov 1978. 101005 (1, <10), 24°19.5′N, 70°24.5′W, 280 m, 27 Feb 1981. 101006 (1, 34), 25°10.3′N, 71°33.0′W, 318 m, 13 Feb 1983. 101007 (1, 30, illustrated), 26°25.1′N, 71°17.4′W, 280 m, 14 Feb 1983. 101008 (2, ca. 12–ca. 22), 26°20.3′N, 71°18.0′W, 232 m, 14 Feb 1983. 101009 (1, <15), 25°41.6′N, 71°31.0′W, 132 m, 15 Feb 1983. 101010 (1), 24°47.1′N, 70°27.0′W, 356 m, 17 Feb 1983. 101011 (1, ca. 12), 24°11.4′N, 70°25.2′W, 303 m, 18 Feb 1983. 101012 (1, ca. 22), 26°20.2′N, 74°12.5′W, 112 m, 26 Feb 1983. 101013 (1, 19), 27°52.0′N, 66°45.7′W, 261 m, 3 Apr 1983. 101014 (1, 39), 26°44.9′N, 66°38.8′W, 260 m, 4 Apr 1983. 101015 (1, ca. 11), 29°56.4′N, 68°58.2′W, 298 m, 16 Mar 1985. 101016 (2, ca. 9–ca. 25), 27°04.7′N, 70°03.4′W, 134 m, 13 Feb 1989. 101017 (1, 11), 27°21.6′N, 70°12.3′W, 299 m, 14 Feb 1989. 101018 (5, 13–15), 27°02.1′N, 73°59.7′W, 304 m, 16 Feb 1989. 101019 (1, 13), 26°33.6′N, 73°53.9′W, 318 m, 19 Feb 1989. 101020 (1, <10), 26°42.7′N, 73°59.4′W, 302 m, 20 Feb 1989. 101021 (1, 19), 26°14.3′N, 73°49.3′W, 300 m, 21 Feb 1989. Note: Another specimen, MCZ 101026 (<15 mm), probably belongs here, but it is badly damaged and we cannot determine the number of gut loops. Pacific (1, 9 mm SL): USNM 324871 (1, 9), 29°48′00″N, 179°03′54″E, 50–100 m, 9 Feb 1985.

Species 2

Figures 1 (middle), 2, 3

Diagnosis. Atlantic specimens (including data from holotype, Schmidt, 1909): Four gut loops. Five expanded melanophores along lateral midline at myomeres 14–16 (4 specimens), 29–31 (4), 44–48 (4), 57–65 (4), 71–78 (4), centered below surface and often extending onto body wall on one side or other; two to four melanophores near dorsal margin of body, in clear area above myomeres. Myomeres: total ca. 108–ca. 130 (4), preanal 65–75 (4).

Pacific specimens: Four gut loops. Four or five expanded lateral melanophores, at myomeres 12–19 (14), 25–38 (14), 42–53 (14), 53–68 (13), 61–75 (7); one or two dorsal melanophores; other pigment as in Atlantic specimens. Myomeres: total ca. 100–110 (9), preanal 57–70 (11).

Size. Atlantic specimens 23–35 mm SL, Pacific specimens ca. 19–43 mm; all premetamorphic. The specimen reported by Raju (1974) was given as 40 mm; we remeasured it as 37 mm.

Variation. Three of the four Atlantic specimens came from the Sargasso Sea, the other (the holotype of *Leptocephalus holti*) from the northeastern Atlantic south of Ireland (Fig. 2). Despite its geographic separation from the others, the holotype shows no obvious differences from the three western Atlantic specimens. The holotype and MCZ 101003 have fewer total myomeres (ca. 108–112) than MCZ 101002 and 101004 (ca. 120–130 and ca. 128). The former pair also has fewer preanal myomeres (65–67 vs. 74–75). In one specimen (MCZ 101003), the last vertical blood vessel enters the kidney slightly more anteriorly than in the others, i.e., in the trough between the third and fourth gut loops instead of near the top of the fourth loop. Another specimen (MCZ 101002) has extra ventral melanophores, between the first–second and second–third gut loops. With the limited material available and the difficulty of obtaining precise myomere counts, we are unable to assess the significance of these differences.

Thirteen of the 15 Pacific specimens came from an area north to northeast of the Hawaiian Islands, one came from Southeast Hancock Seamount in the central North Pacific, and one from the South Pacific, southwest of the Austral Islands (Fig. 3). The South Pacific specimen is at the low end of the range of a few meristic characters (preanal myomeres, position of some lateral melanophores), but the only character that is clearly outside the range of the other specimens is the position of the fifth lateral melanophore (61–62 vs. 64–75). Seven specimens have four lateral melanophores, seven others have five, and one has three. Tabeta's (1988) specimen has five lateral melanophores, and its total and preanal myomere counts (99 and 59, respectively) fall within the range of our specimens. The Pacific specimens appear to have fewer total myomeres (99–110) and preanal myomeres (57–70) than the Atlantic specimens (ca. 108–130 and 65–75, respectively). The position of the first four lateral melanophores coincides in the Atlantic and Pacific specimens. Only the fifth appears to differ, at myomere 61–75 in the Pacific vs. 71–78 in the Atlantic specimens. All four Atlantic specimens have five lateral melanophores, whereas more than half of the Pacific specimens examined by us have only three or four.

Material Examined. Atlantic (3, 23–26 mm SL): MCZ 101003 (1, 26 illustrated), 28°31.4′N, 69′02.1′W, 475 m, 4 Mar 1981. 101002 (1, 23), 26°59.7′N, 68°52.0′W, 150 m, 23 Mar 1985. 101004 (1, 23), 31°27.0′N, 64°21.0′W, 9 Apr 1990. Pacific (15, 19–45 mm SL): LACM 36437-1 (1, 28), 26°32′N, 147°13′W, 0–160 m, 10 Apr 1966. 36438-2 (1, ca. 21), 26°32′N, 147°13′W, surface, 10 Apr 1966. 36447-4 (1, ca. 24), 27°55′N, 144°10′W, 11 Apr 1966. 36454-3 (1, 22), 28°48′N, 141°59′W, surface, 12 Apr 1966. SIO 70-118 (1, 37, specimen described by Raju, 1974), 24°30.5′S, 154°54′W, 0–175 m, 4 Oct 1969. 89–57 (2, 42–43), 31°N, 159°W, 200–0 m, 13–14 Apr 1989. 89-63 (4, 19–39), 31°N, 159°W, 200–0 m, 18 Apr 1989. 89-65 (2, 42–42), 31°N, 159°W, 400–0 m, 19 Apr 1989. 89-68 (1, 34), 31°N, 159°W, 0–900 m, 22 Apr 1989. USNM 324872 (1, 26), 29°49′46″N, 179°07′54″E, 0–100 m, 20 Apr 1987.

Species 3

Figures 1 (bottom), 2, 3

Diagnosis. Three gut loops, including hepatogastric swelling. Lateral and dorsal pigment absent; paired melanophores on lateral surface of gut adjacent to pectoral fin; a melanophore dorsally and one on each side of hepatogastric swelling; a complex melanophore dorsally on the two posterior gut loops, extending laterally on each side of gut; no melanophore between second and third gut loops; pigment present at tip of snout and lower jaw. Myomeres: total ca. 104–115 (4), preanal ca. 54–57 (6).

Size. Largest specimen ca. 25 mm; all specimens premetamorphic.

Variation. Five specimens came from the Sargasso Sea and one from the central North Pacific. Significant variation is not evident.

Material Examined. Atlantic (5, 16–ca. 25 mm SL): ANSP 153490 (1, 19), 21°03′N, 57°54′W, 0–150 m, 30 Mar 1979. MCZ 101022 (1, 23), 26°17.1′N, 66°44.6′W, 253 m, 8 Apr 1983. 101023 (1, 25, illustrated), 26°17.0′N, 66°45.0 W, 150 m, 9 Apr 1983. 101024 (1, 23), 28°31.4′N, 69°02.1′W, 302 m, 17 Mar 1985.

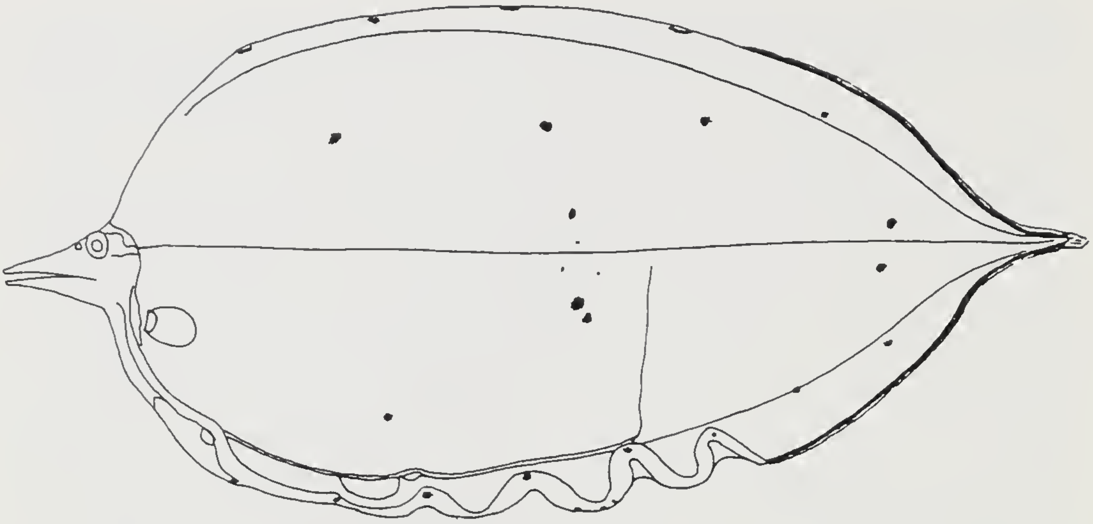

Figure 4. Leptocephalus of *Cyema atrum* (after Smith, 1989b).

101025 (1, 16), 27°02.1′N, 73°59.7′W, 304 m, 16 Feb 1989. Pacific (1, 10 mm SL): USNM 324783 (1, 10), 29°47′36″N, 179°03′54″E, 50–100 m, 9 Feb 1985.

IDENTIFICATION AND RELATIONSHIPS

Leptocephalus holti and the larva of *Cyema atrum* (Fig. 4) share the following characters: a long, peg-like snout with a straight profile; a posteriorly placed eye; a gut with an anterior swelling at the hepatogastric region followed by two to four arches or loops; pigment dorsally on each gut loop; pigment near the dorsal margin of the body; an acute tail without distinct hypural elements; a large ventral blood vessel conspicuously separated from the gut tube; and V-shaped myomeres with a highly obtuse angle at the midlateral line. These characters distinguish *Cyema atrum* and *L. holti* from all other leptocephali and support the hypothesis that they belong to the same family. *Cyema atrum* (Fig. 4) has a deeper body than *L. holti* with a steeper anterior profile, it has an expanded mass of pancreatic tissue that fills much of the space between the dorsal margin of the intestine and the ventral margin of the myomeres, and its lateral pigment is scattered over the side of the body instead of being restricted to the midline.

If *L. holti* is accepted as a cyematid, which cyematid is it? Both Castle (1977:75) and Smith (1989b:947) have made the obvious suggestion that *L. holti* is the larva of *Neocyema,* but they considered such an identification inconclusive. Particularly troublesome was the absence of any trace of the conspicuous lateral melanophores in the specimens of *Neocyema,* despite the semileptocephaloid appearance of the latter. Bertin (1937:17) showed that the lateral pigment of the leptocephalus was retained in a 115-mm juvenile *Cyema atrum.* Both the holotype of *L. holti* and Raju's Pacific specimen had conspicuous lateral pigment. Castle in particular felt that the pigment character made an identification of *L. holti* with *Neocyema* unlikely. Smith agreed but pointed out that the age of the *Neocyema* specimens was unknown and that at least some specimens of *L. holti* lacked lateral pigment.

The present material further reduces the objections to identifying *L. holti* as the larva of *Neocyema.* It is now clear that the majority of Atlantic *L. holti* lack lateral pigment, so the main obstacle has been removed, at least in theory. The number of myomeres is in the same range (Castle [1977] reported that the one intact specimen of *Neocyema erythrosoma* had 108 total myomeres). Although the identification cannot be disproved, it cannot be confirmed, either, especially in the absence of metamorphic specimens. The only known specimens of *Neocyema* were taken far from the known range of *L. holti,* but lack of adequate collecting weakens this objection. After all, for more than 60 years *L. holti* was known from a single specimen.

Larval fishes can provide important and valuable information that is not available from the study of adults alone. Regardless of whether *L. holti* is the larva of *Neocyema* or another still unknown genus, these larvae enable us to say without question that such a genus exists, it contains at least three species, and it is found in all oceans.

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BREVIORA

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THE GENUS *PHENACOSAURUS* (SQUAMATA: IGUANIA) IN WESTERN VENEZUELA: *PHENACOSAURUS TETARII,* NEW SPECIES, *PHENACOSAURUS EUSKALERRIARI,* NEW SPECIES, AND *PHENACOSAURUS NICEFORI* DUNN, 1944

TITO R. BARROS,[1] ERNEST E. WILLIAMS,[2] AND ANGEL VILORIA[1]

ABSTRACT. Two new, possibly parapatric species of *Phenacosaurus* are described from the Sierra de Perijá, Estado Zulia, Venezuela: *P. tetarii,* larger, at least 85 mm snout–vent length, with heterogeneous squamation on the flanks, closest to *P. nicefori* but larger in adult size, and *P. euskalerriari,* small, about 56 mm snout–vent length, with uniform flank squamation, closest to *P. orcesi,* but with larger flank scales and shorter interparietal.

Phenacosaurus nicefori Dunn is redescribed on the basis of material from Betania, Estado Táchira, Venezuela, and from the Páramo de Tamó, overlapping the borders of both Colombia and Venezuela, as well as from topotypic material from Norte de Santander in Colombia.

INTRODUCTION

The members of the genus *Phenacosaurus* are anoline lizards endemic to the subpáramo and páramo of northwestern South America and are characterized by a casqued head with converging lateral parietal crests with a smaller or larger notch at their occipital ends, a variable vertebral crest, short limbs, and a probably prehensile tail. Initially they were believed to be present only in Colombia, from where the type species, *Phenacosaurus heterodermus,* was described by Duméril and Duméril in 1851. Dunn (1944), studying material in Colombian collections, added two new species to the genus, *P. nicefori* from the Department of Norte de Santander and *P. richteri* from the Department of Cundina-

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marca. Hellmich (1949) described as *P. paramoensis* a single specimen from the páramo overlapping the borders of the Departments of Cundimamarca, Huila, and Meta. Lazell (1969), in a revision using most of the known specimens of the genus, synonymized *P. richteri* and *P. paramoensis* with *P. heterodermus* but added the species *P. orcesi* on the basis of two specimens from Ecuador. The first giant species of the genus from the Cordillera Oriental of Colombia was named *P. inderenae* by Rueda and Hernández-Camacho (1988). Williams and Mittermeier (1991) cited a juvenile from Venceremos in the Department of San Martin in Peru as a possible third specimen of *P. orcesi.*

At the present time, several additional new species of the genus have been described or are in the process of description. From Venezuela, Myers *et al.* (1993) described a small series of one new species (*P. neblininus*) from the Cerro La Neblina in the extreme south, and Williams *et al.* (1996b) described an additional new species based on a single specimen collected by S. Gorzula and A. Farrera in the Macizo del Chimantá Tepui in Estado Bolivar. A second giant species very similar to *P. inderenae* has been collected in La Alegría and adjacent localities in the Provincia de Sucumbíos in Ecuador and was described by Williams *et al.* (1996a).

As the result of three expeditions to the Sierra de Perijá in Estado Zulia, Venezuela, in 1989 and 1991 by the Museo de Biologia of the Universidad del Zulia (MBLUZ), four specimens of *Phenacosaurus* (MBLUZ R-215 and R-308, MCZ 176474, and 176475) represent two new species. One species is represented by a male from the Páramo de Tetari and a female from the Cerro Pintado. A specimen (MHNLS 664) of this new species had already been collected by Ramón Urbano in 1952 but was referred to *P. nicefori* by Alemán (1953) and Lazell (1969). The other is a smaller species, again a male and a female, related to *P. orcesi.*

In addition, with the intention of completing a synopsis of the species of *Phenacosaurus* in western Venezuela, the material of *P. nicefori* from Betania, Estado Táchira, and Páramo del Tamá, which overlaps both the Department of Norte de Santander of Colombia and Estado Táchira, Venezuela, and also topotypic specimens from the Department of Norte de Santander, Colombia, are reported and described.

The descriptions of the new species herein are a slightly modified version of the format utilized by Williams for lizards of the genus *Anolis* (for the nomenclature of the scales, see Williams *et al.*, 1996a,b).

DESCRIPTION

Phenacosaurus tetarii, new species

Holotype. MBLUZ R-215, adult male, collected by Angel Viloria, October 24, 1989, on the roads that lead to the Páramo del Tetari, Sierra de Perijá, Estado Zulia, Venezuela (10°06′34″N, 72°53′00″W), 2,790 m elevation.

Paratypes. MHNLS 664, adult male, collected by Ramón Urbano, 1952, at the base of Pico Tetari, Sierra de Perijá, Estado Zulia, Venezuela, 2,900 m elevation; MCZ 176474, adult female, collected by Angel Viloria, March 24, 1989, at the base of Cerro Pintado, Sierra de Perijá, Estado Zulia, Venezuela, 2,400 m elevation.

Etymology. Tetari is the name that the Yukpa Indians have given to the second highest peak in the Serranía de Perijá (3,575 m elevation).

Diagnosis. A phenacosaur closest to *P. nicefori* but differing in the greater snout–vent length (SVL of *tetarii*: holotype male 80 mm male, paratype 86 mm; female 70 mm, rather than a maximum SVL of males 57 mm and females 58 mm in *nicefori*), with the parietal area converging to a very narrow notch at its occipital margin, and differing also in the dewlap color (*tetarii*: yellow rather than white with pale orange stripes in *nicefori*).

Description. The description is based primarily on the male holotype and the male paratype; the differences of the female paratype are mentioned whenever visible.

Head: A casque well developed. The head scales anteriorly mostly smooth, but strongly pustular posteriorly in the region of the parietal table.

Dorsal head scales (Fig. 1)—Antorbital area: Canthals 4 on both sides in both males, 4 on the left side in the female paratype, the other side obscure. In the male holotype, the anteriormost canthal separated from the circumnasal by 3 small scales on the left side, by 2 scales on the right side. In the male paratype in this area at

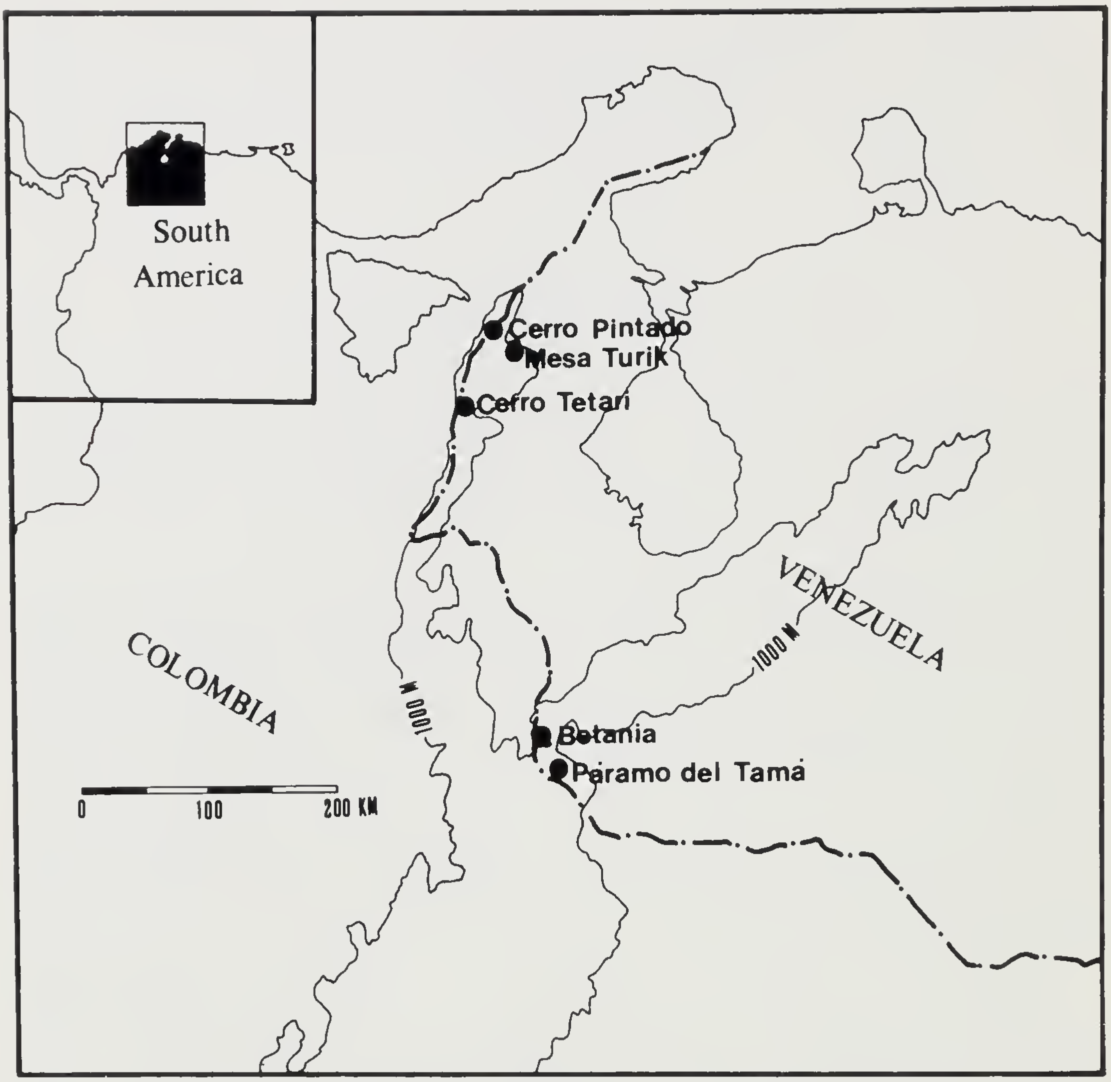

South America
Cerro Pintado
Mesa Turik
Cerro Tetari
COLOMBIA
VENEZUELA
1000 M
1000 M
Betania
Páramo del Tamá
0
100
200 KM

Figure 1. Map of the localities mentioned in this paper.

least 6 small scales on the left, 5 on the right. In the female paratype 2 scales on the left, 1 on the right. Four scales between the second canthals in all specimens. Rostral wider than high, bordered posteriorly by 4 or 6 postrostrals, 2 of which are in contact with the first supralabials. The circumnasal on each side in contact with the first supralabial and separated from the rostral by the postrostral that overlies the sulcus between the first supralabial and rostral. In the male holotype dorsally between the circumnasals, a single large scale in a central position posterior to the postrostrals, flanked by 2 smaller scales. In the female paratype 2 subequal scales in this position. In the male paratype 6 scales in 2 rows. Between the second canthals 2 (male holotype) the largest scales of the head and, indeed of the entire animal, 3 (male and female paratypes).

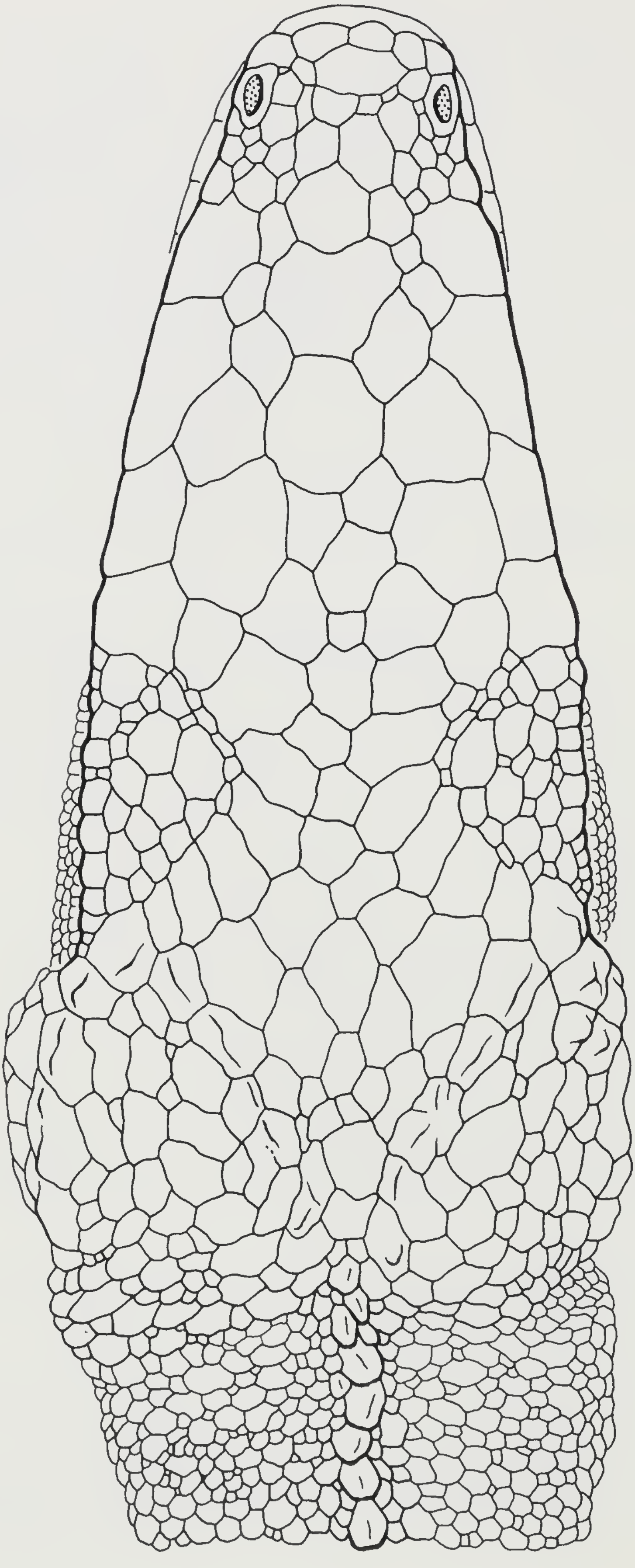
Orbital area: The supraorbital semicircles separated by 1 row of moderately sized subrectangular scales in the holotype male. In the male paratype 1 anterior row in contact. In the female paratype 2 posterior pairs in contact. In all specimens both the scales of the semicircles and those of the median row being bluntly tubercular or ridges that may be coalesced tubercles. All the scales of the supraocular area much smaller than those of the semicircles, quite smooth, and differing much in size, larger medially, smaller laterally. The largest, also the most medial on both sides, in narrow contact with the semicircles in the male holotype on the right. In the male paratype all, including the largest, of the medial supraoculars in contact with all the semicircles. The female paratype obscure.

Parietal area: Low ridges separating the rounded convex supratemporal area and the relatively depressed and flat parietal table, converging straight back to end in low bosses that leave a narrow notch between them. The scales of the ridges very bluntly keeled and intermediate in size between the mostly large smooth scales of the supratemporal area and the uniformly small and strongly pustulate scales of the parietal table.

The interparietal scale, inferred to be such because of its shape and anterior medial placement, small, rhomboid in the male holotype, more irregular in shape in the female and male paratypes, all specimens without a parietal eye. In the male holotype and the male paratype interparietal separated from the supraorbital semicircles by 1 scale on each side, almost as large or larger than itself. In the female the interparietal in contact with both adjacent scales of the semicircles. Four or 5 scales between the interparietal and the nape scales.

Lateral head scales (Fig. 2)—The lateral head scales all smooth except for the lateral faces of the posterior canthals, which are pustular like their dorsal surfaces.

One to 3 rows of loreal scales, counted just in front of the preoculars. The anterior of these always in single rows. The total number of loreals only 6 on 1 side, 7 on the other in the male holotype, the male paratype 6 on both sides, 8 on both sides in the female paratype. Two preoculars on each side in all specimens.



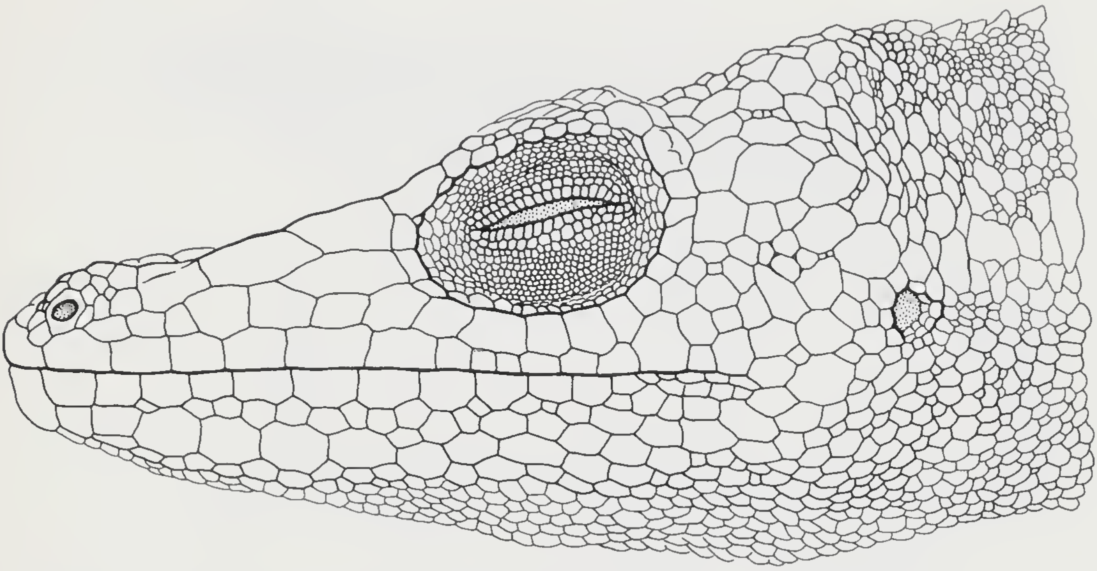


Figure 3. *Phenacosaurus tetarii,* holotype, MBLUZ R-215: Lateral view of head.

Eight supralabials to below the center of the eye in the male holotype, 9 in the male paratype, 10 in the female paratype. Six to 9 postoculars on each side arch round the back of the orbit, the uppermost in contact dorsally with the posteriormost scale of semicircle of its side and laterally with the posteriormost superciliary.

The temporal region divided into supra- and infratemporals by an intertemporal ridge, covered by 2–4 scales. The ridge strongly convex but not shelf-like.

The supratemporals larger, but variable in size close to the parietal ridges, smaller near the intertemporal ridge. The infratemporals are larger close to the intertemporal ridge, smallest in a narrow zone in the center of the region, then again larger, almost as large as the uppermost infratemporal scales in a band from the ear to the corner of the mouth.

The ear small, inconspicuous, smaller than many of the scales surrounding it, smaller also than the inferred interparietal.

Ventral head scales (Fig. 3)—The mental incompletely divided, in contact with only 2 differentiated sublabials between the in-

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Figure 2. *Phenacosaurus tetarii,* holotype, MBLUZ R-215: Dorsal view of head.

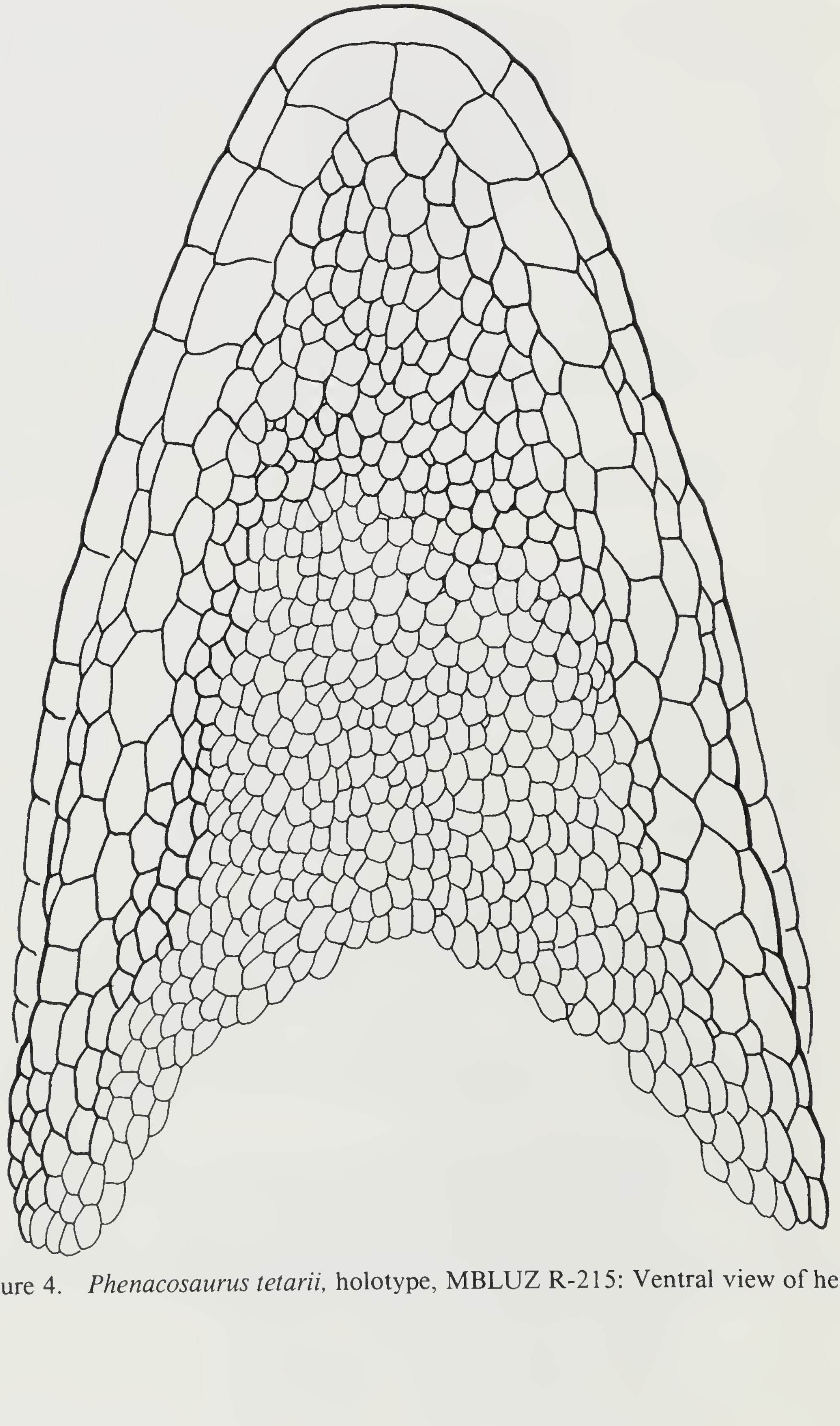

Figure 4. *Phenacosaurus tetarii,* holotype, MBLUZ R-215: Ventral view of head.

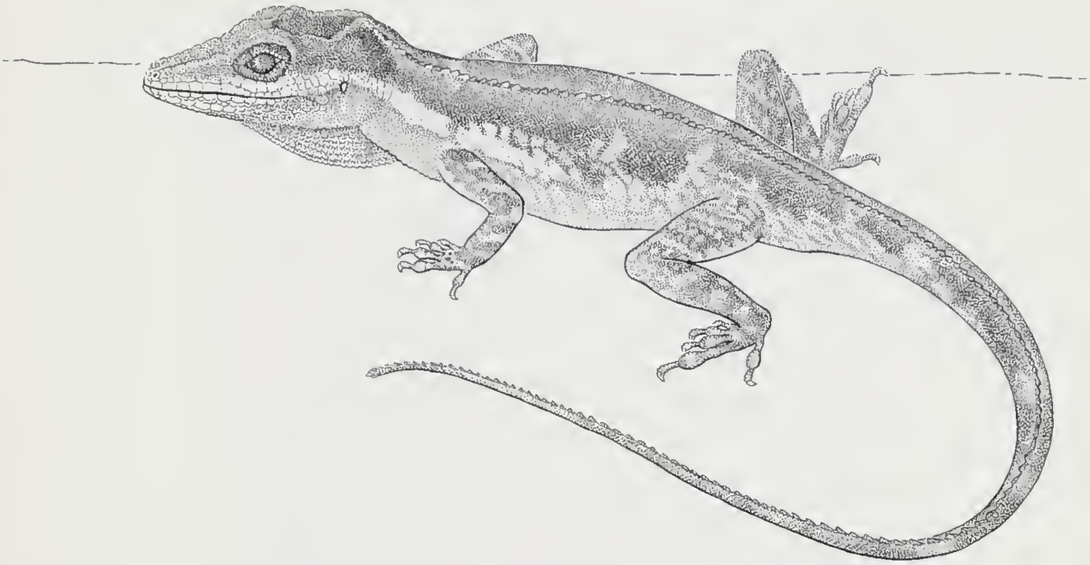

Figure 5. *Phenacosaurus tetarii,* holotype, MBLUZ R-215: Lateral view of entire animal.

fralabials (male holotype and male paratype). Five sublabials on each side in contact with the infralabials in the male holotype, the first sublabials only by their corners. In the male paratype 2 sublabials are in contact with the infralabials, 3 on the left. The female paratype obscure. The swollen medial gulars grading posteriorly into swollen gulars less than half their size.

Trunk (Figs. 4 and 5): The middorsal scales, a dorsal crest of Type 3 *sensu* Lazell (1969, fig. 1), a single series of vertebral scales, swollen keeled cones, at irregular intervals each such scale separated from other vertebrals by a pair of flat or slightly swollen paravertebrals that meet middorsally. In the male the sequence of the 2 types of middorsals is nearly regular until the region of the sacrum, where the cones are in contact. About 4–5 rows of paravertebrals, rounded and flat, varying somewhat in size, in contact or slightly overlapping and showing little or no intervening skin. Below this on each flank a zone of distinct granules, mostly fully separating round flat scales that differ little from the paravertebrals in size but tend to be somewhat smaller. Below this, beginning at about the middle of the flank patches of slightly larger round flat scales in partial contact appear; they appear to be concentrated in irregular areas that are more lightly pigmented than the rest of the flank. Ventrals smooth and strongly imbricate,

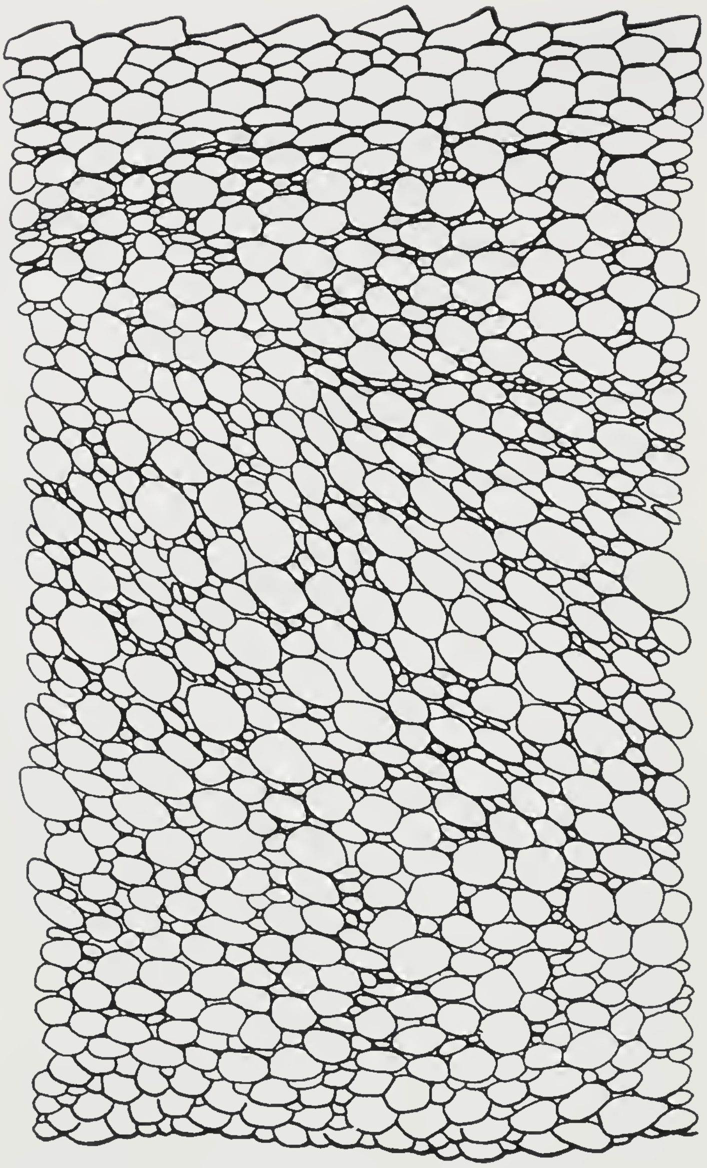

Figure 6. *Phenacosaurus tetarii,* holotype, MBLUZ R-215: Flank scales behind shoulder.

bluntly pointed and about equivalent in size to the round flat scales of the flanks.

Limbs (Fig. 4): All limb scales smooth, differing primarily in size. The scales of the anterior face of upper arm and of the thigh

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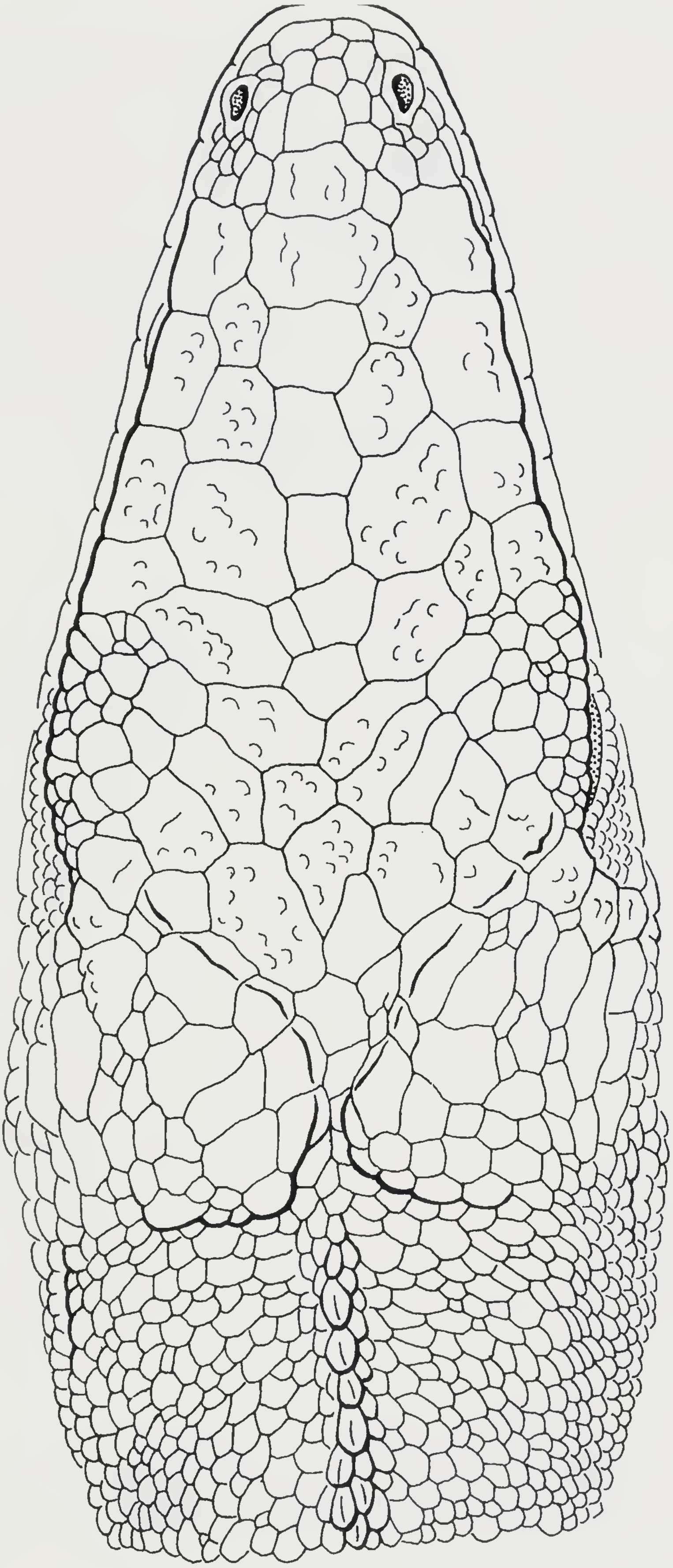
Figure 7. *Phenacosaurus tetarii,* male paratype, MHNLS 664: Dorsal view of head.



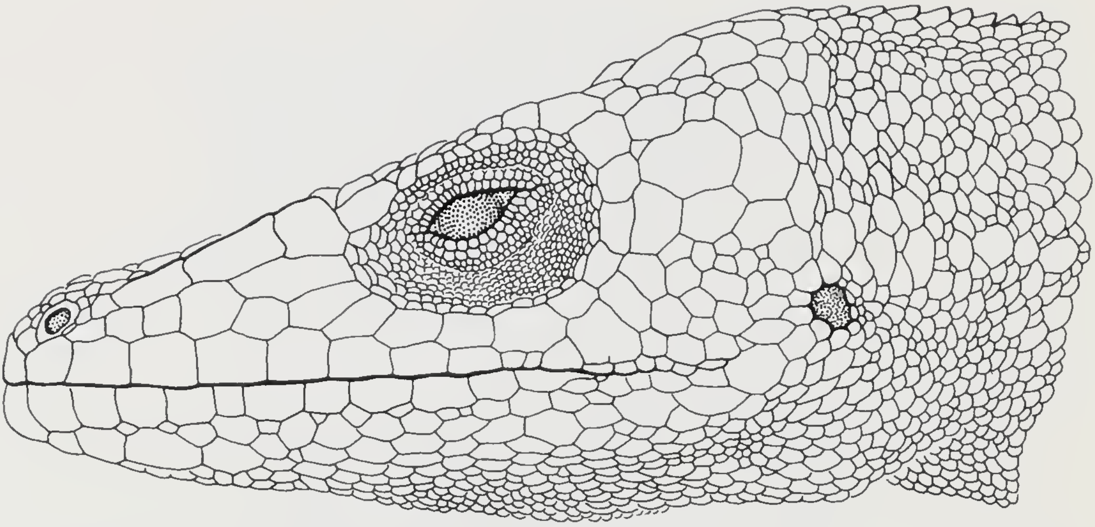


Figure 8. *Phenacosaurus tetarii,* male paratype, MHNLS 664: Lateral view of head.

distinctly larger than those of the posterior face, especially on the thigh, where the posterior scales are almost granular. The scales of the lower arm and tibia not differing much in size on the anterior and posterior surfaces. The digital scales of both hands and feet with the dorsal and ventral surfaces lamellar—wider than long, and overlapping distally—throughout the length of the digits. The adhesive lamellae under phalanges ii and iii of the fourth toe 23 in the male, not determinable in the female.

Tail (Fig. 4): Tail curved and apparently prehensile. All caudal scales, except those at the very tail base, keeled, most sharply ventrally. At the base the crest scales keeled cones as large as and very similar to those of the middorsal sacral area. Farther back on the tail the crest scales become more elongate, lower, and smaller and toward the end of the tail indistinguishable from the other scales of the tail except that they are on the middorsal line of the tail. As on the dorsum, the series of caudal crest scales is interrupted by the medial juncture of paravertebral caudals, but in this case the paravertebrals are keeled and the interruptions are few and at highly irregular intervals.

Dewlap (Fig. 4): Dewlap in both sexes relatively small, extending posteriorly a little farther than the level of the axilla, densely scaled, the swollen scales about the size of the ventrals.

Color in Life. (The patterns shown in Figure 4 are long after

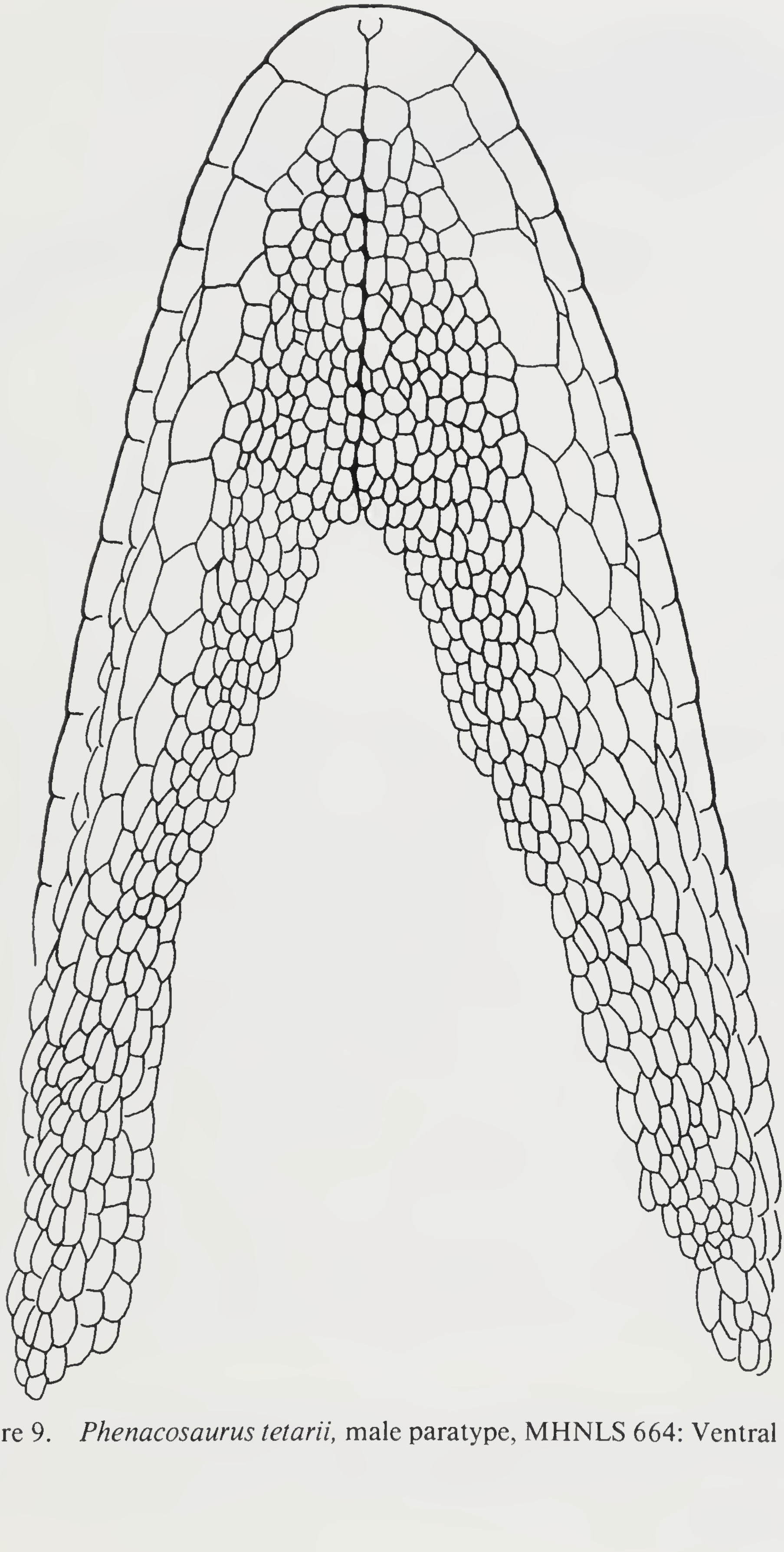


Figure 9. *Phenacosaurus tetarii,* male paratype, MHNLS 664: Ventral view of head.

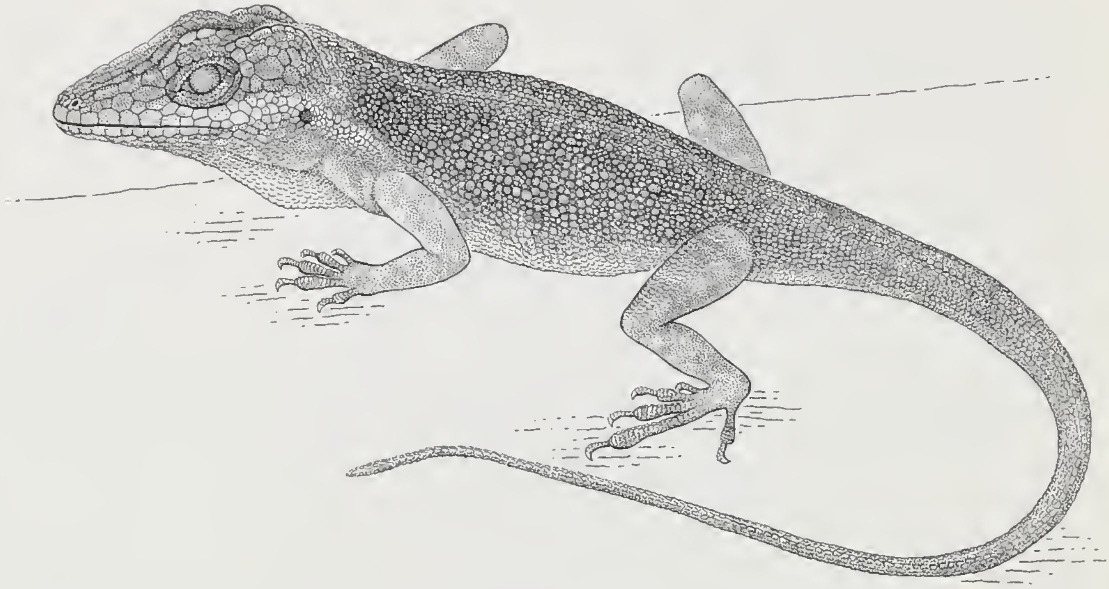


Figure 10. *Phenacosaurus tetarii,* male paratype, MHNLS 664: Lateral view of entire animal.

preservation.) The color of the holotype was described shortly after preservation, when the darker tones had been accentuated by the preserving liquid. From the parietal region to the tip of the tail, the dorsum was dark brown (sepia No. 119) (Smithe, 1975). There were five rounded blotches on the dorsum from the nape to the insertion of the hindlimbs, the distances between these spots being about 5 mm. These spots were light cream (light drab No. 119C), but reference to photographs (slides) of the live animal shows that in life the color was much more yellow (buff-yellow No. 53), as was the color of the belly and the throat. The head from the tip of the snout to the beginning of the parietal region was a dark olive green (grayish yellow No. 430). The limbs have the color of the dorsum but with some transverse bars of an orange color (ferruginous No. 41), especially on the anterior limbs. There was a white band on each side of the head running from the supralabials and loreals to the flanks at midbody. Belly light, the

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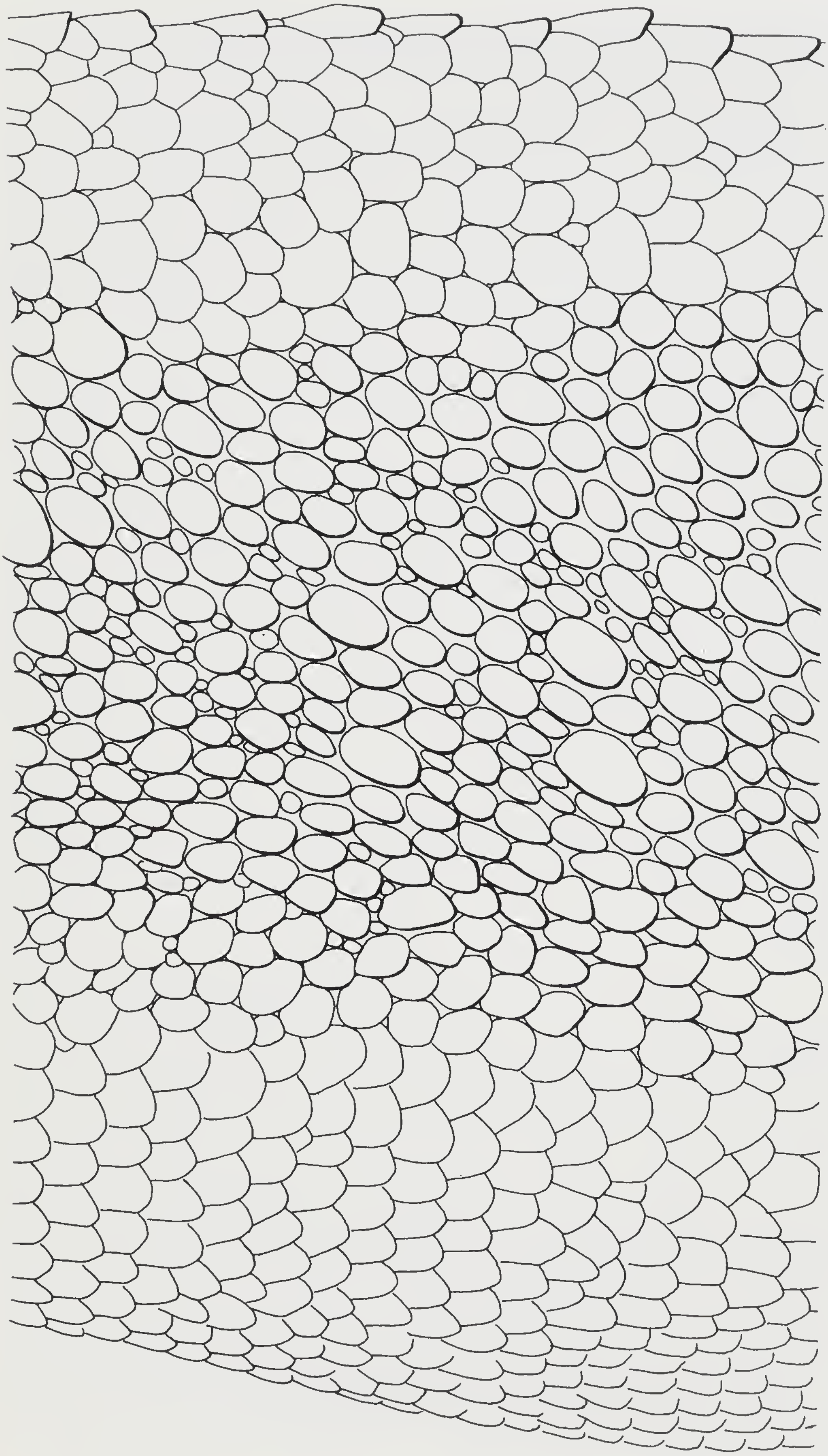
Figure 11. *Phenacosaurus tetarii,* male paratype, MHNLS 664: Flank scales behind shoulder.



scales lightly spotted with black and brown. The tail dark brown (sepia No. 119) with lighter transverse bands.

The dewlap is yellow.

Sex Dimorphism. There are problems in inferring sex dimorphism with only three specimens available. The males (two specimens) (>80 mm) appear to be larger than the female (one specimen) (69 mm), which is certainly mature because it laid an egg (15 × 10 mm). The male holotype was much more brown than green, whereas the single female was a general light green in color. This apparent color difference is problematic because there is just one other specimen (the MHNLS paratype) for which the color in life has not been reported.

Habitat. The female paratype was collected on a shrub; the male holotype was encountered on spongy lichens and dead leaves. Both specimens were collected in stunted forest in the ecotone between cloud forest and the shrubby páramo. The low trees have very tangled and leathery branches, and the region is cloudy during the greater part of day. *Phenacosaurus tetarii* probably inhabits exclusively the higher cloud forest and the lower limits of the páramo at elevations between 2,200 and 3,000 m.

Distribution. This is a species endemic to the Sierra de Perijá and restricted to the higher altitudes that constitute the border between Colombia and Venezuela and known from two localities 22 km apart, the Páramo del Tetari and the massif of Cerro Pintado.

Phenacosaurus euskalerriari, new species

Holotype. MBLUZ R-308, adult male, collected by Jon Ugarte, March 22, 1991, in the canyons of Mesa Turik, Sierra de Perijá, Estado Zulia, Venezuela (72°44′27″W, 10°22′23″N), 1,600 m elevation.

Paratype. MCZ 17475, adult female, collected by Javier Zabala, March 17, 1991, in the Campamento de la Gran Depresión of Mesa Turik, Sierra de Perijá, Estado Zulia, Venezuela (72°42′48″W, 10°24′10″N), 1,700 m elevation.

Etymology. Euskalerriari signifies, in the Basque language, "of the Basques." The name is proposed for this new species in honor of the expedition "Vasco-venezolana Turik 1991," during which these specimens were collected.

Diagnosis. A phenacosaur closest to *P. orcesi* but differing in the shorter length of the interparietal, the aspect of the scales surrounding the interparietal, the size of the uniform flank scales and the higher lamellar count, and possibly in the blue dewlap (blue is a very unusual dewlap color, and the color of the *orcesi* dewlap is unknown).

Description. As in the previous description, this description is primarily based on the male holotype; the female is mentioned only when differences are clearly visible.

Head: Dorsal head scales (Fig. 12)—Antorbital area: Scales smooth or weakly rugose, smaller toward the tip of the snout. Six squarish or rectangular postrostrals. Circumnasals in broad contact with the first supralabials of each side and separated from the rostral by the outermost postrostrals. Dorsally 4 scales between the circumnasals.

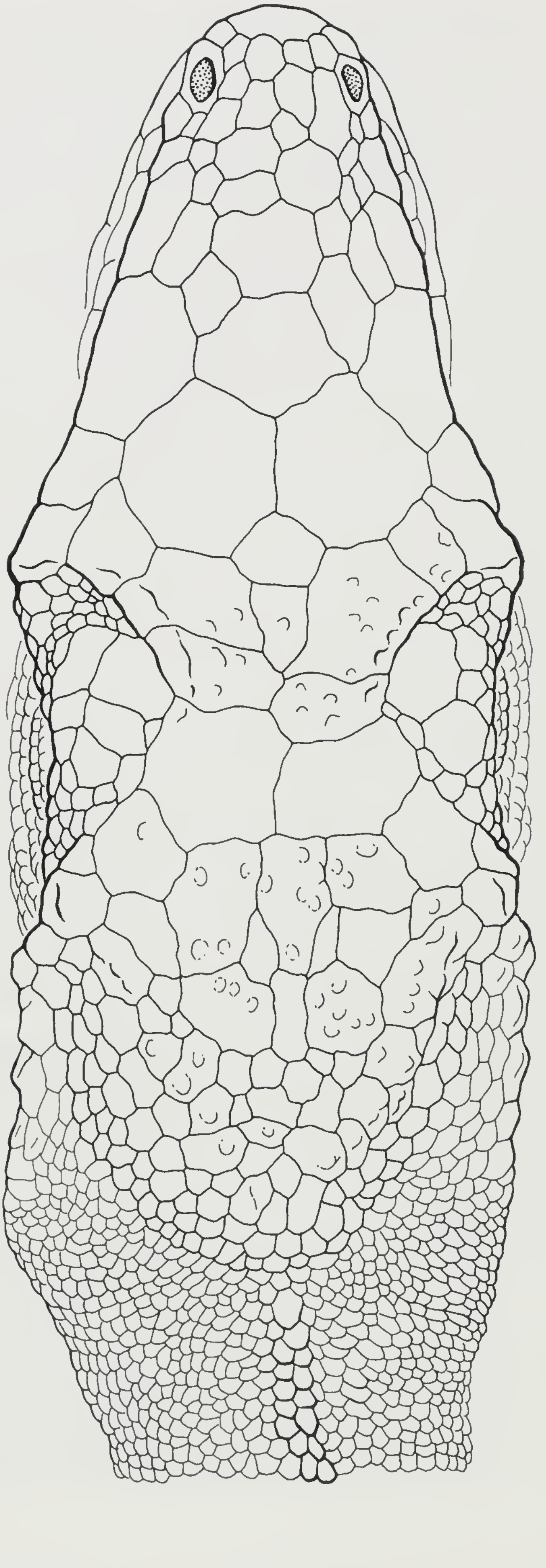
Canthal scales, 6 on each side, the anteriormost in contact with the circumnasal of its side. Two scales between the second canthals in the male holotype, in the female paratype 3 scales. The frontal depression very shallow, formed by parts of 4 large scales in the male holotype, parts of 6, only slightly smaller scales, in the female.

Orbital area: All scales of the semicircles heavily tuberculate, except the 2 most posterolateral in the male holotype. The anteriormost and posteriormost of each side form prominent bulges in front and behind the orbit, and the lateral edges of these and other scales of the semicircles slightly raised in rounded ridges, circumscribing the supraocular area.

The scales of the supraocular area smooth or slightly rugose. The largest supraocular on each side in contact with the supraorbital semicircles. The supraoculars grading in size mediolaterally. Superciliaries small and smooth, grading in size from larger anteriorly to granular posteriorly.

Parietal area: The converging boundary ridges of this area begin as strong tuberculations on flat or only slightly convex scales adjoining the posteriormost scales of the semicircles. The tuberculate or pustulate boundary ridges converge to meet posteriorly in 2 small raised blunt bosses at midline. Notching in this case minimal, merely the groove between the 2 bosses.

Lateral head scales (Fig. 13)—Most lateral scales smooth, but



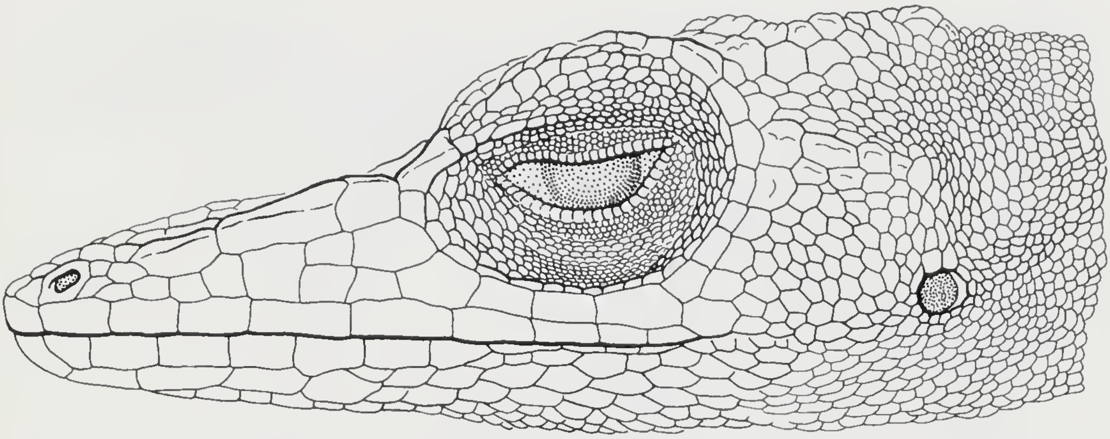


Figure 13. *Phenacosaurus euskalerriari,* holotype, MBLUZ R-308: Lateral view of head.

the lateral faces of 2 canthals, the scales of the intertemporal ridge and the postoculars more or less heavily tuberculate, some suboculars weakly tuberculate. In the male, 2 rows of loreals—total of 8—on each side, arranged as follows, counting from the front a single row of 5 scales, increasing in size posteriorly, a double row of 2 scales one precisely above the other, then again a single row, 1 scale underneath the single preocular. In the female on the right side, precisely the pattern seen in the male; on the left side, however, only 6 loreals, with the single preocular in contact not only dorsally with the second canthal, but also in ventral contact with fifth and sixth supralabials.

One preocular on both sides in both specimens. Three suboculars on both sides in the female, and also on the right side in the male, but 4 on the left. Both posteriormost suboculars in the female with 2 or 3 tubercles. Seven heavily tuberculate postoculars. The suboculars broadly in contact with the supralabials. Seven supralabials to below the center of the eye on both sides of both specimens.

The intertemporal ridge moderately prominent, covered by 4 scales, each with 1 or more tubercles. Supratemporals and infratemporals smooth and flat, moderate in size.

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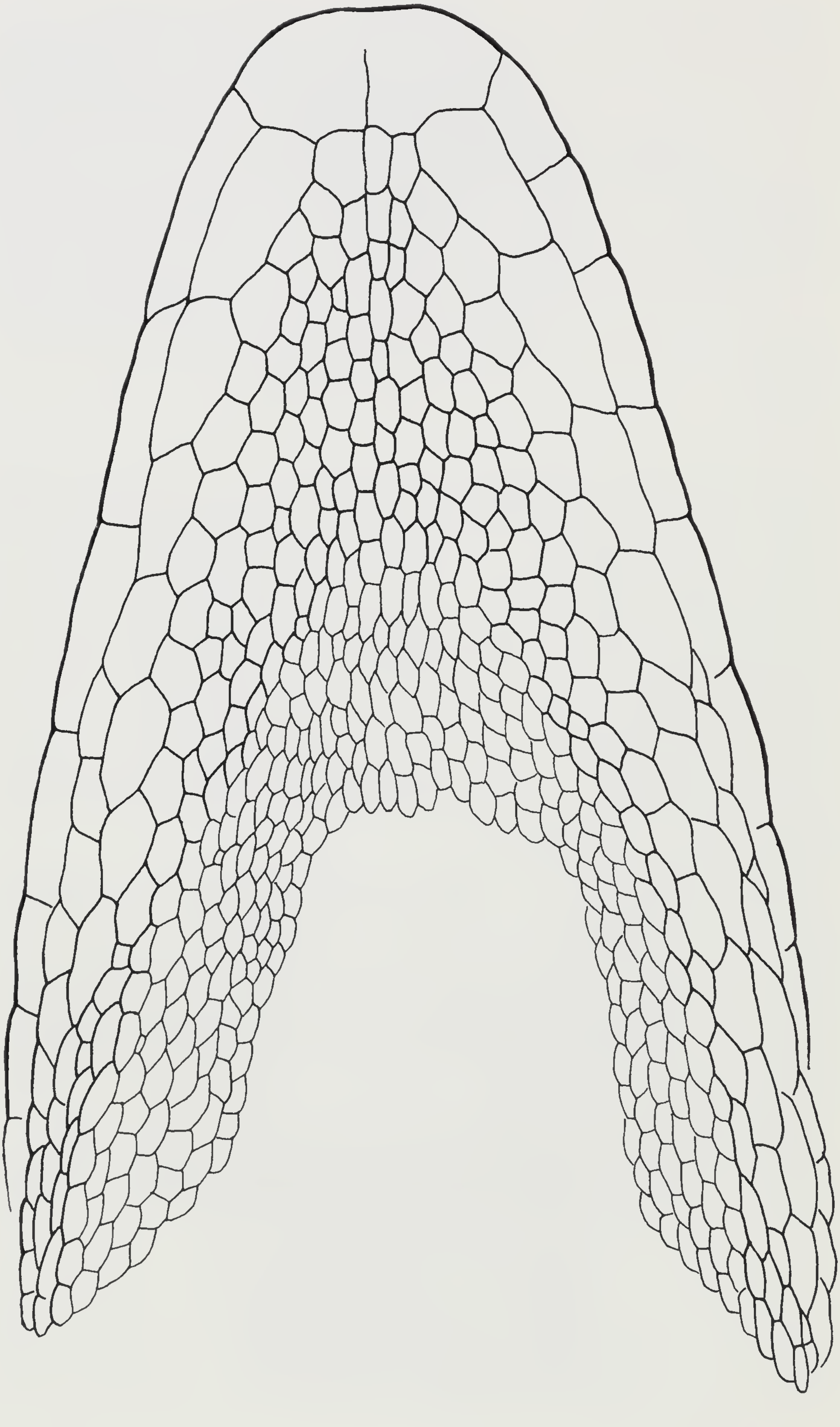
Figure 12. *Phenacosaurus euskalerriari,* holotype, MBLUZ R-308: Dorsal view of head.



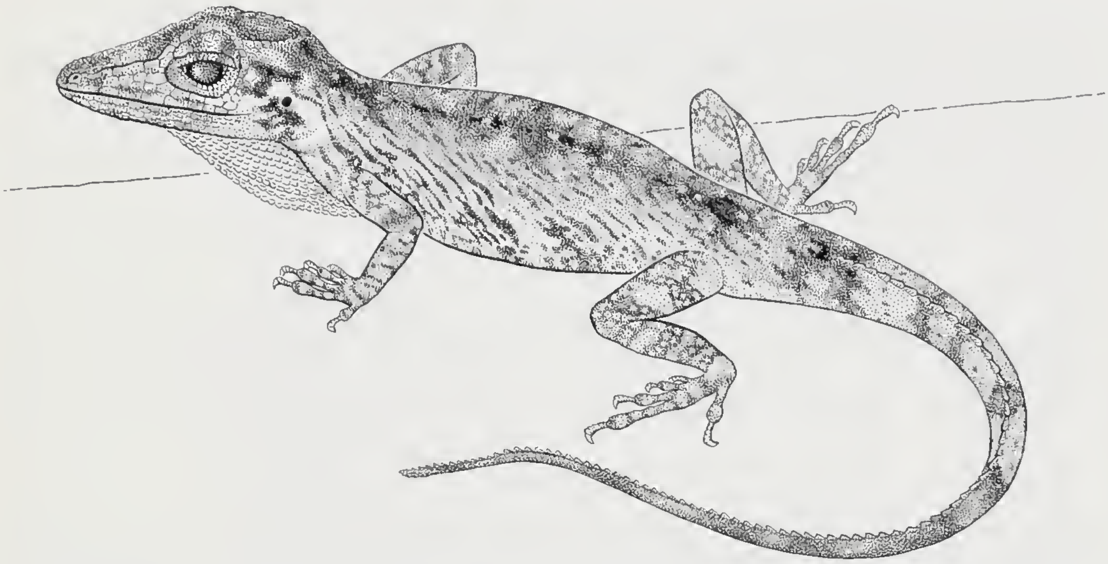


Figure 15. *Phenacosaurus euskalerriari,* holotype, MBLUZ R-308: Lateral view of entire animal.

Ear conspicuous, oval or ovoid, the greater dimension vertical, larger than adjoining scales, smaller but not greatly smaller than interparietal.

Ventral head scales (Fig. 14)—Mental semidivided in male with a nearly transverse posterior margin. Five postmentals (2 of them differentiated sublabials) between the infralabials. Three or 4 scales in the sublabial series on each side are in contact with infralabials. The postmental gulars larger than the more posterior central gulars but smaller than the rows of labials just medial to the sublabials.

Trunk (Figs. 15 and 16): No dorsal crest in either specimen, but on the nape patches of very low subconical scales. At middorsum and meeting in the midline hexagonal smooth scales only little larger than and very little different from the uniform flank scales. Ventrals smooth, larger than dorsals, subimbricate, and in transverse rows.

Limbs (Fig. 15): All limb scales smooth, but differing in size. Those of the anterior faces of upper and lower arms and of thigh

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Figure 14. *Phenacosaurus euskalerriari,* holotype, MBLUZ R-308: Ventral view of head.

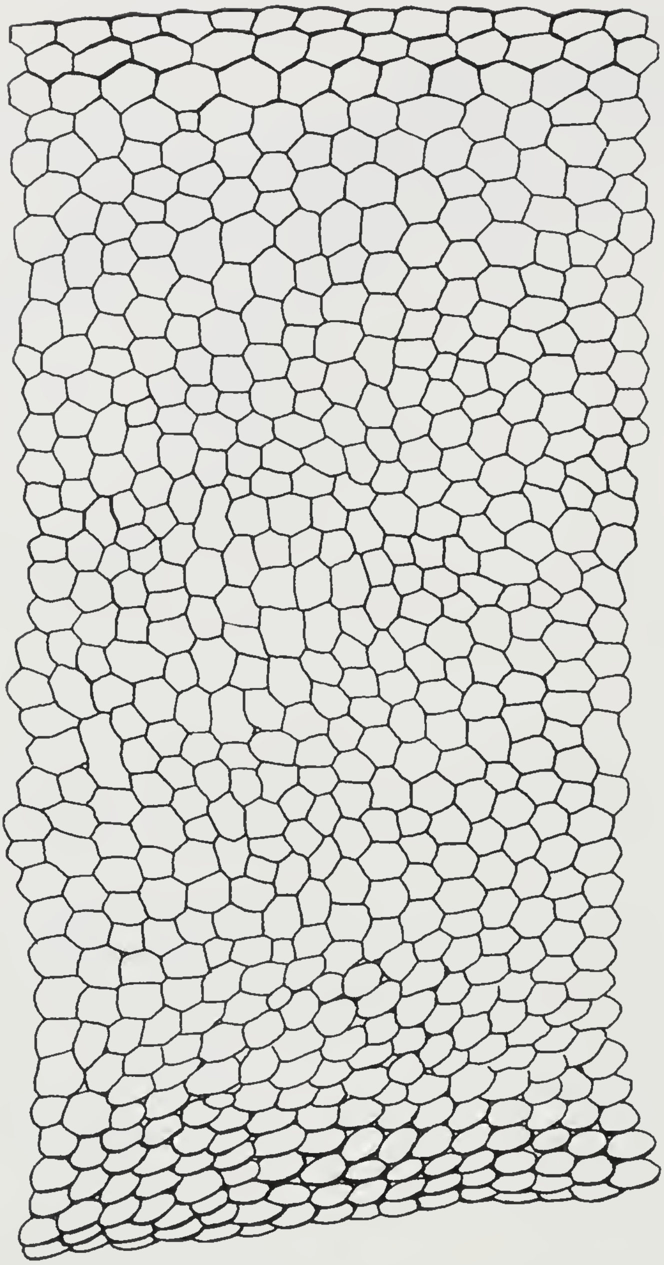


Figure 16. *Phenacosaurus euskalerriari,* holotype, MBLUZ R-308: Flank scales behind shoulder.

and tibia about as large as flank scales, their ventral and posterior faces more nearly granular. The digital scales of both dorsal and ventral surfaces are lamellar—wider than long, and overlapping distally throughout the length of all digits. The adhesive lamellae under phalanges ii and iii of fourth toe 21 in the male and 25 in the female.

Tail (Fig. 15): The tail strongly compressed, curved, apparently prehensile. Large postanals in the male only. A distinct crest of keeled swollen scales begins at the base of the tail, where the scales are small then distinctly larger beyond the tail base, but decreasing gradually in size to tail tip. Lateral scales smooth and small. Four midventral rows of keeled scales begin about 30 scales behind postanals.

Dewlap (Fig. 15): Dewlap posterior to the insertion of the arms in both sexes. Edge scales are smaller than ventrals in the male. The lateral scales are in rows separated by relatively wide wrinkled areas of naked skin.

Color and Pattern. The male is shown by a slide to have a general emerald green coloration (emerald green No. 163) marked irregularly with brownish (dark drab No. 119BB), very likely highly cryptic in its habitat. Head brownish in the parietal area and at the tip of the snout. On the flanks more prominent brown blotches that project on the belly as triangles that resemble the peaks of a mountain range. The tail is banded green and brown. The limbs present the same pattern as the body.

The dewlap is light lead-colored blue.

Habitat. This species inhabits the forests of Perijá and has been encountered at approximately 1,700 m elevation, both specimens on bushes in scrub/dwarf forest. It appears to be a species of the cloud forests below 2,000 m in elevation, and its coloration of green and brown in life suggests a cryptic aspect appropriate to its silvicolous habit. In view of the altitudinal amplitude of the cloud forests in which it lives, the species could be distributed between 1,600 and 2,500 m elevation, uniquely in very humid forests. It is possible then that it is parapatric with the larger species of higher and more open formations.

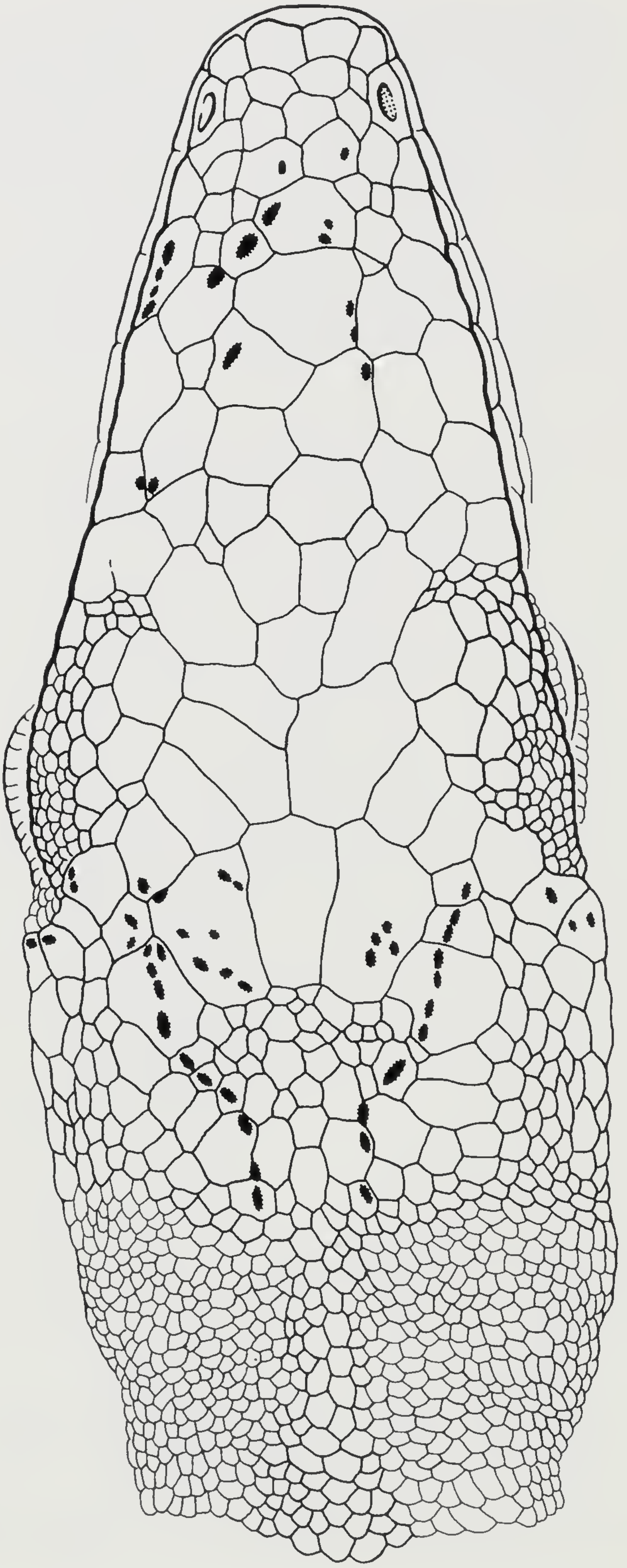
Distribution. P. euskalerriari is known only from the Mesa Turik (1,600–2,300 m), a limestone meseta, located between the Río Apón and the headwaters/origins of the Río Palmar on the Venezuelan slopes of the Sierra de Perijá, Estado Zulia, Venezuela.

Phenacosaurus nicefori Dunn

Phenacosaurus nicefori Dunn, 1944, Caldasia, **3:** 59. Type: ILS 64.

Type Locality. Pamplona, Norte de Santander, Colombia.

Diagnosis. Smaller than *Phenacosaurus heterodermus* and *P. tetarii* (maximum SVL: male 63 mm, female 58 mm) and differing from the giant species and *P.*



heterodermus by fewer large (as does *P. tetarii*) round flat scales on the flanks and with the posterior notch between parietal crests especially wide, wider than any other species in the genus.

Description. Head: Dorsal head scales (Fig. 17)—Antorbital area: Six to 8 canthals; if 7 or 8, 1–2 small canthals have been intercalated in the series. The third canthal largest. One small scale or none between anteriormost canthal and the circumnasal. Four to 5 squarish scales border the rostral posteriorly. The circumnasal on each side in broad contact with the first supralabial and separated from the rostral by 1 postrostral or in contact. Four scales between the circumnasals dorsally. Small scales behind the circumnasals occur in 1 or 2 rows medial to the anterior canthals.

Orbital area: The scales of supraorbital semicircles always at least weakly tuberculate. There are 1 or 2 pairs in contact, or 2 scales on one side may contact with one on the other. The scales of the supraocular area, which are always smooth, decrease in size laterally. Two or 3, rarely 4, of the larger supraoculars are in contact with the semicircles medially. These scales are separated from the superciliary margin by 2–3 granular rows. Superciliaries are mostly subgranular, but the 1 or 2 anteriormost of the series are slightly larger.

Parietal area: Lyre-shaped and tubercular lateral parietal ridges arise from the scales that are in contact with the posteriormost scales of the supraorbital semicircles and terminate in bluntly swollen boss-like scales separated by low, wide notch, relatively wider and lower than in other species of the genus. All scales of parietal table distinctly lower than the bounding parietal ridges and more or less strongly tuberculate. Interparietal with or without an eye, larger than the very small ear, round, subrhomboid or subhexagonal, are separated from the semicircles by 1 or 2 scales or in contact. Scales lateral to the interparietal tend to be about as large as the interparietal. Four to 6 scales intervene between interparietal and the notch, which is filled by a transverse row of 2–3 smooth scales.

Lateral head scales (Fig. 18)—There are 1 or 2 rows of loreals; if 2, the upper row is posterior only or is intercalated at intervals above the lower row. Total loreals vary from 4 to 9. Only 1 preocular is present, usually small and in contact only with the anterior subocular and the second canthal; if larger and additionally in contact with the sublabial series, it perhaps implies a fusion of a lower loreal with the preocular. There are 4–5 suboculars and 6 to 8 usually tuberculate postoculars. Seven to 9 supralabials extend to below the center of the eye.

A moderately prominent intertemporal ridge is covered by 3 or 4 scales. Supratemporals smooth, mostly small, largest toward the parietal ridges. Infratemporals smooth, mostly largest near the intertemporal ridge and toward the corner of the mouth.

Ventral head scales (Fig. 19)—Mental semidivided, in contact with 4 postmentals between the infralabials: 2 sublabials, 1 on each side and 2 medial gulars.

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Figure 17. *Phenacosaurus nicefori*, KU 181131, Betania, Táchira, Venezuela: Dorsal view of head.

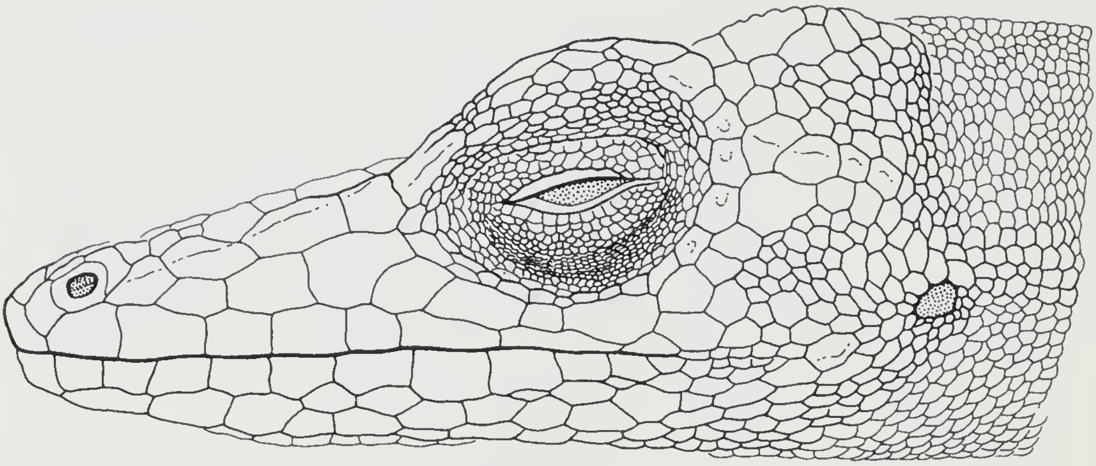

Figure 18. *Phenacosaurus nicefori,* KU 181131, Betania, Táchira, Venezuela: Lateral view of head.

Three or 4 of the sublabial series on each side in the contact with the infralabials. Central gulars smooth, small, longer than wide or as wide as long, juxtaposed, becoming larger polygonal adjacent to the sublabial series.

Trunk (Figs. 20 and 21): Dorsal crest variable, absent or interrupted (Type 3 of Lazell) or consisting of adjoining keeled scales on the middorsum. On the nape, the crest usually comprises small cones irregularly arranged. Flank scales are smooth, juxtaposed or even subimbricate, sometimes weakly separated, variable in size, but the larger round scales are relatively few. Ventrals smooth, imbricate to subimbricate, in transverse rows.

Limbs (Fig. 20): Limb scales smooth, including supradigitals. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 15–22.

Tail (Fig. 20): Tail weakly compressed. Enlarged postanals present in the male. A Type 3 or Type 4 crest on the tail, with the crest scales much larger than laterals, about as large as 2 ventralmost rows. Lateral scales are weakly rugose, becoming distinctly keeled before midlength. The 4 ventralmost caudal scale rows are keeled, the 2 medial ventral rows largest, a bit larger than the scales of the tail crest.

Dewlap (Fig. 20): In the male extending a short distance posterior to the level of the axilla, densely scaled, with crowded rows of scales. In the female represented by a densely scaled fold extending only to the level of the axilla.

Color in Life. There is just one description of color in life for a specimen that we have examined. It is by William Duellman for a specimen (KU 181130) from Betania on the eastern slopes of Cerro Tamá, Estado Táchira, Venezuela: "Dorsum grayish tan to dark brown. Labial region and venter creamy white. Dewlap creamy white with pale orange stripes." A slide shows that the dorsum is banded.

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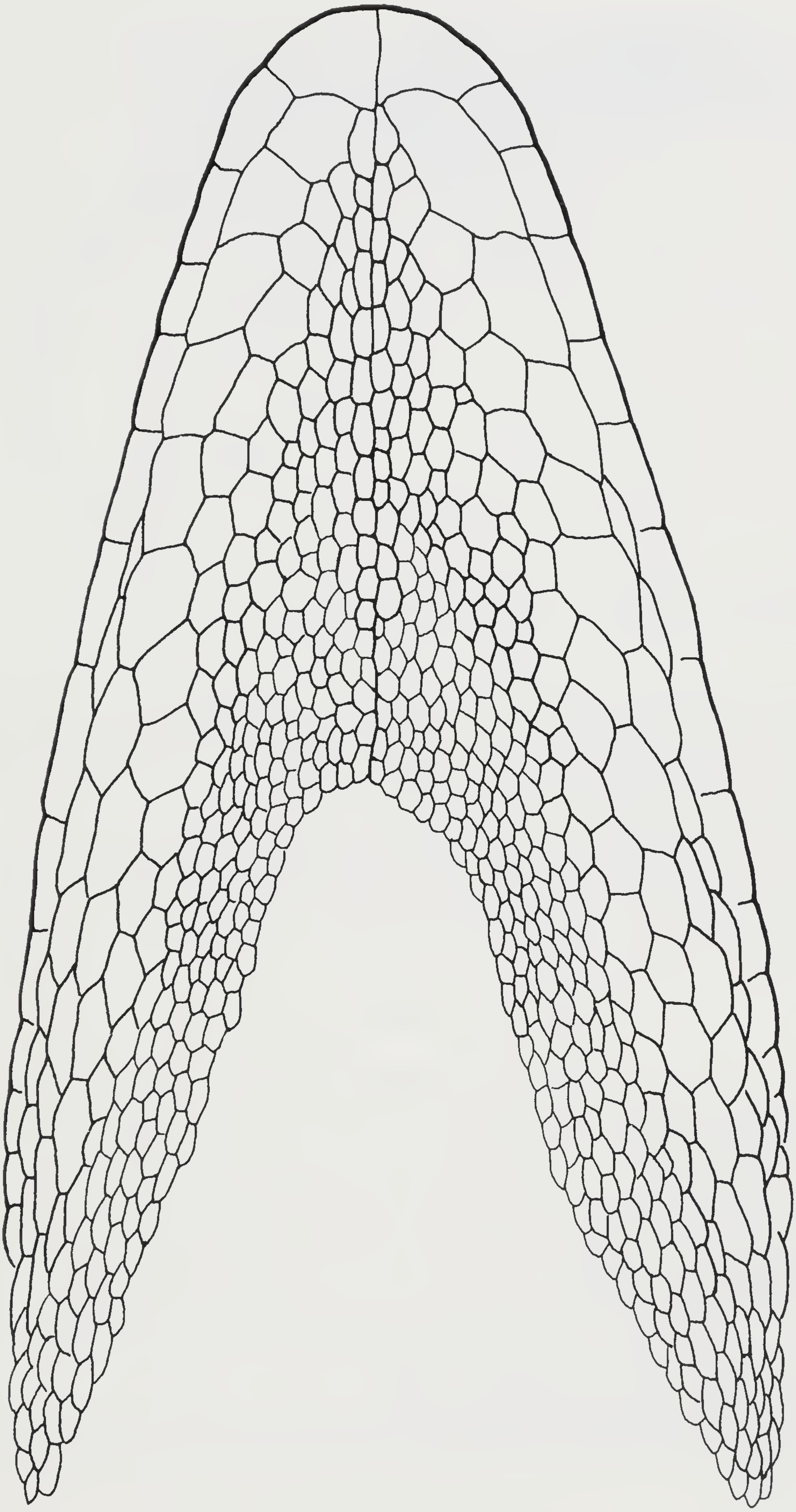
Figure 19. *Phenacosaurus nicefori,* KU 181131, Betania, Táchira, Venezuela: Ventral view of head.



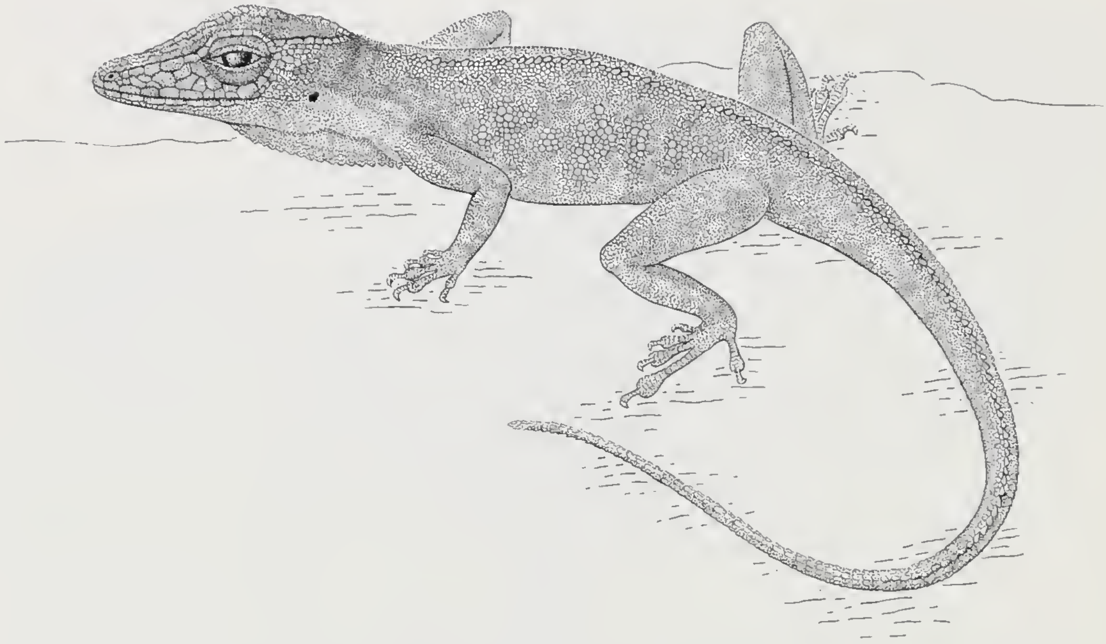


Figure 20. *Phenacosaurus nicefori,* MCZ 67979, Pamplona, Norte de Santander, Colombia: Lateral view of entire animal.

Habitat. This species inhabits the high-Andean humid forest in an altitudinal band between 2,000 and 2,600 m above the level of the sea in the Colombian Cordillera Oriental and in Venezuela in the Páramo de Tamá, which occupies parts of two states, Estado Táchira and Estado Apure.

Individuals perch on small shrubs and bushes or on moss.

Material Examined. VENEZUELA: Estado Táchira: Betania, altitude 2,150 m: CVULA IV 0898-218V-219-VJEP; CVULA IV 0899-220-VJEP; KU 181130–132; Páramo de Tamá, altitude 2,400 m: MCN 4529, FMNH 5684; COLOMBIA: Departamento Norte de Santander: Pamplona.

MUSEUM ABBREVIATIONS

CVULA = Colección de Vertebrados de la Universidad de los Andes, Mérida, Venezuela
KU = Kansas University, Museum of Natural History, Lawrence, Kansas, USA
MBLUZ = Museo de Biologia de la Universidad de Zulia, Maracaibo, Venezuela
MCN = Museo de Ciencias Naturales, Caracas, Venezuela
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MHNLS = Museo de Historia Natural La Salle, Caracas, Venezuela

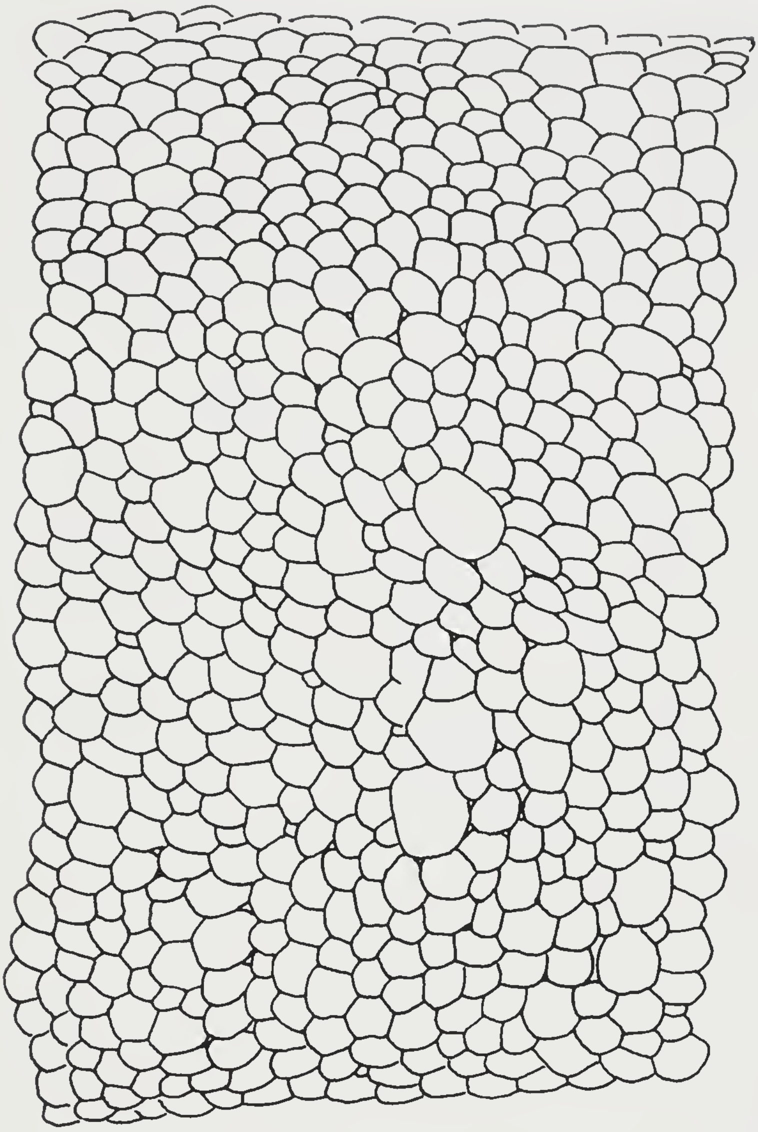


Figure 21. *Phenacosaurus nicefori,* Betania, Táchira, Venezuela: Flank scales behind shoulder.

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A NEW GIANT PHENACOSAUR FROM ECUADOR

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Juan Carlos Matheus,[3] and Robert Bleiweiss[4]

Abstract. A new giant *Phenacosaurus* from the eastern Andes (La Bonita–Santa Bárbara Region) of Sucumbíos Province of Ecuador is described. It, like *P. inderenae* Rueda and Hernandez, 1991, differs from all other species in reaching a maximum size of more than 100 mm and differs from *inderenae* in the smaller size of the largest class of heterogeneous scales (flat flank scales interspersed with smaller scales and granules). In the density of the largest class of scales, it resembles *heterodermus* and differs from *nicefori* Dunn, 1944, and *tetarii* Barros, Williams, and Vilora, 1996. From all the remaining species, it differs in having heterogeneous scales.

INTRODUCTION

The first giant phenacosaur, *Phenacosaurus inderenae* (>100 mm in snout–vent length [SVL]), was described by Rueda and Hernández–Camacho (1988) from Gutiérrez, in the southeast of the Department of Cundinamarca, Colombia, on the eastern slopes of the Cordillera Oriental of the Andes, syntopic or sympatric with *P. heterodermus.*

Since that description, there has been an explosion of information concerning these lizards. New species belonging to several subgroups have been described: *tetarii* Barros, Williams, and Viloria, 1996, and *euskalerriari* Barros, Williams, and Viloria, 1996, both from the Venezuelan side of the Cerro de la Perijá; *neblininus*

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Myers, Williams, and McDiarmid, 1993, from the Cerro de la Neblina, at the border of Brazil and Venezuela; and an unnamed juvenile (Williams and Mittermeier, 1991) from Venceremos, Department of San Martin, Peru. Two more require description, a second giant from Ecuador, formally described herein, and another small species from Chimantá Tepui, Venezuela (Williams, Praderio and Gorzula, 1996).

Sorting out at least the similarities and differences of the several new described and undescribed species within the genus seems necessary at this time. The justification of the genus will be postponed until a separate paper.

It has only been possible to separate *P. inderenae* and the species described later by comparing the whole type series of *inderenae* with the whole type series described later. Both type series are small, four in the case of *inderenae,* eight (but one was found dead and is now a skeleton) in the new species later, but each comes from a well-defined local area. We find that the large, flat, round scales are consistently smaller in the Ecuadorean species as compared with *P. inderenae* and, on that basis, describe the former as a new species. To facilitate future research, we have described the holotype separately and in detail. We discuss variation within the remainder of the type series of the new species in the same format as the description of the type, except that we describe a probable hatchling separately. We then deal with the variation in the type series of *inderenae* in the same style and format.

The material of the new species is deposited in four museums: the type and the first found of the paratypes (now a skeleton) in the Museo Ecuatoriano de Ciencias Naturales (MECN), four of the paratypes in the Escuela Politecnica Nacional (EPN), two of the paratypes in the Museum of Comparative Zoology, and one paratype in the National Museum of Natural History (USNM).

The new species, which is very close to *P. inderenae* in many characters in addition to size, is here named for the distinguished Brazilian scientist, Paulo Emilio Vanzolini.

Phenacosaurus vanzolinii, new species

Holotype. MECN 0309, adult male.

Type Locality. ECUADOR: S La Alegría, at an elevation of 2,360 m, ca. 14 km by road from La Bonita (77°37′42″W,

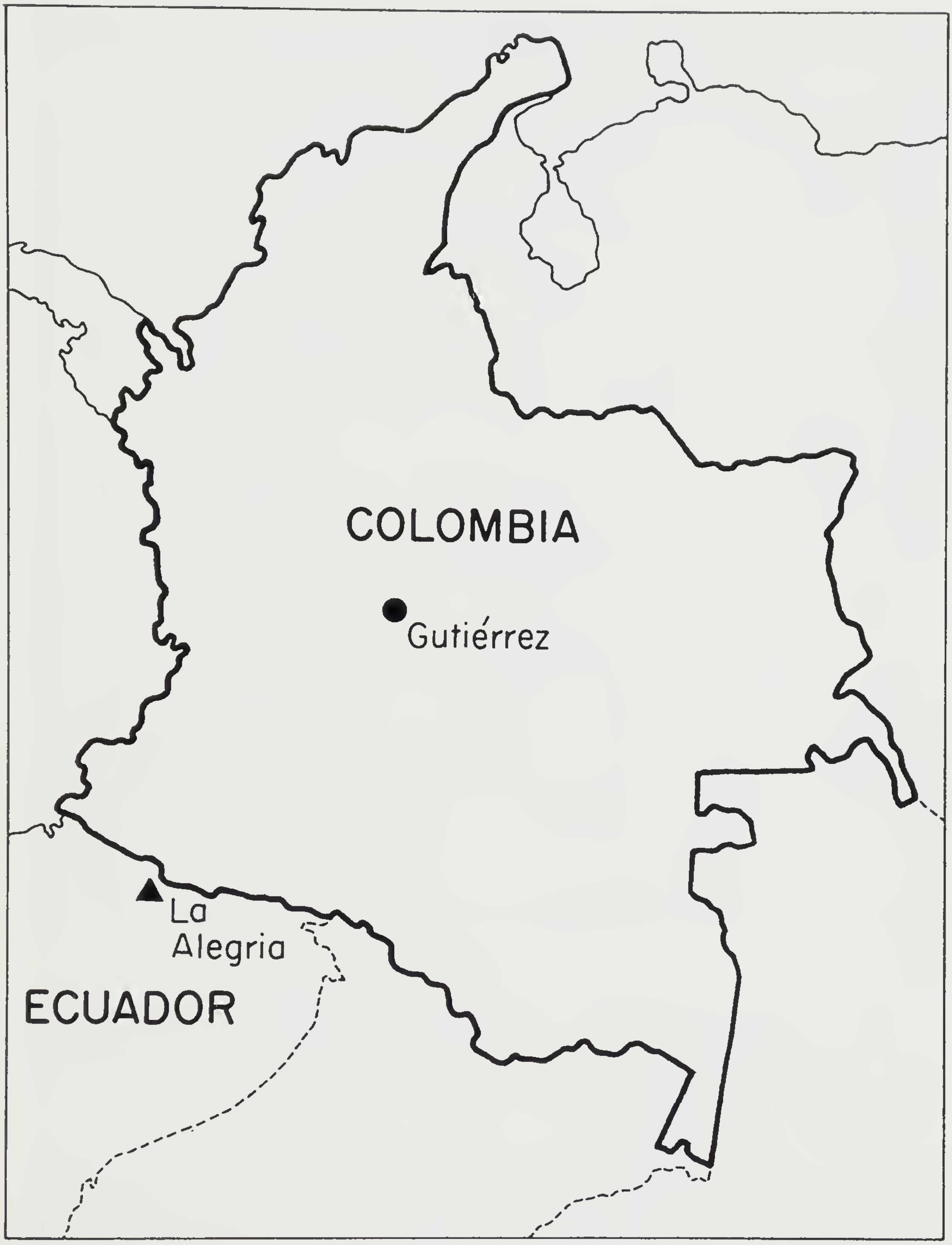
COLOMBIA
Gutiérrez
La Alegria
ECUADOR

Figure 1. The regions of the type localities of *Phenacosaurus inderenae* (circle) and *Phenacosaurus vanzolinii* (diamond).

0°27′30″N), Provincia de Sucumbíos (formerly the northwest part of Provincia de Napo), Robert Bleiweiss and Juan Carlos Matheus coll. 15 March 1985.

Paratypes. All ECUADOR: Provincia de Sucumbíos: MECN

0327: found dead in the road (now a broken skeleton), at the same locality as the type, Juan Carlos Matheus coll. 1986, sex undetermined; EPN 2218: Sitio Las Ollas, 4 km S Sebundoy, on a road that was opened by heavy machinery when the road was constructed, Ana Almendáriz and Alicia Arias coll. 21 May 1988, a juvenile male, possibly a hatchling; EPN 2219: Sitio Sebundoy, 100 m from the concrete bridge over the Río Chingual on the new road to La Bonita, Ana Almendáriz and Alicia Arias coll. 21 May 1988, adult male; EPN 2221: Sitio Sebundoy, elevation 1,950 m, 6 km N Escuela de Sebundoy, adult male; MCZ 175159 (formerly EPN 2220): adult male with extruded hemipenes, same data as EPN 2221; MCZ 175160: Sta. Bárbara (77°31′41″W, 0°37′58″N), SE Parroquia El Carmelo. Relatives for Janira Regelado coll. 1988. Janira Regelado don. 1989, adult male with extruded hemipenes; USNM 293683: same data as MCZ 175160.

Diagnosis. A giant species, exceeding 100 mm in maximum SVL, resembling *P. heterodermus, P. inderenae, P. nicefori* and *P. tetarii* in the presence of large, round, flat flank scales that at least on the lower flanks are more or less widely separated by granules; differing from *P. orcesi* and *P. neblininus,* in this regard; differing from *P. heterodermus, P. nicefori, P. orcesi,* and *P. neblininus* in maximum adult size, in the posterior height of the casque, and in color pattern and from *P. inderenae* by smaller scales of the largest flank class, as well as of larger posterior lateral gular scales.

Description of Holotype. Head: Head with massive casque. Swollen rugose parietal crests on each side angle obliquely posteromedially to end in 2 knobs connected by an intervening notch, although lower than the knobs, high above the nape.

Dorsal head scales (Fig. 2)—Antorbital area: Scales, pustulate posterolaterally, smooth anteriorly, moderately large except for a single small scale in the shallow frontal depression and one zone of small scales posterior to the circumnasals, another such zone on each side between the anterior canthals and the medial series

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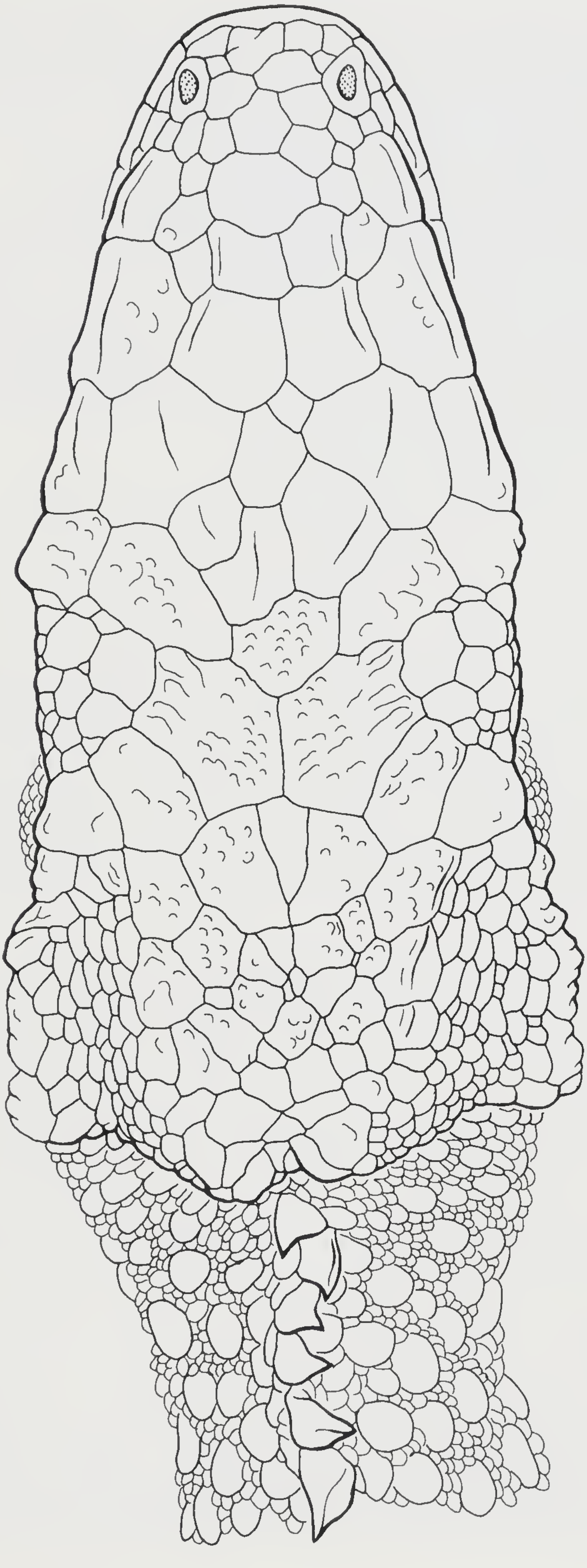
Figure 2. *Phenacosaurus vanzolinii,* holotype, MECN 0309, Dorsal view of head.



of large scales. Circumnasals oval, nostrils slightly posterior within the scales, the acute end of each scale in contact with the first supralabial. A subtriangular postrostral separating each circumnasal from the rostral. Five postrostrals.

Frontal depression shallow. A rosette of larger scales, very weakly rugose or pustulate, around a small smooth scale about equivalent in size to the small scales of the snout. Three or 4 scales across the snout between the second canthals. Canthals swollen, their edges raised and very rugose, apparently covering bony encrustations, four on each side, the third largest and expanded medially, the anteriormost smallest, separated from the circumnasal of its side by 2 superimposed small scales.

Orbital area: Scales of the semicircles very large, rugose and pustulate, 1 pair in broad contact. A single large pustulate scale anterior to this contact. Supraocular scales very much smaller, very finely shagreened, 4 scales on the left side, 6 on the right side in rather well-defined supraocular disks, the 2 largest scales in contact with the semicircles. The anteriormost superciliaries of both sides largest, subtrapezoidal, the whole surface exposed dorsally, the remaining 6 or 7 superciliaries smaller, quadrangular, in a single row mostly on lateral face of head, barely exposed dorsally. The remainder of the supraocular surfaces filled by scales smaller than those of the supraocular disks, larger than the superciliaries.

Parietal area: Scales very variable in size and shape, moderate to small, most lightly rugose but distinctly pustulate. Lateral crest scales very rugose, indicating bony ornamentation underneath, arising abruptly from the low central parietal area, sloping upward toward the posterolateral bosses that are the borders of a moderate but narrow notch. Three smooth scales across the median notch. The several scales covering the two eroded posterolateral bosses also smooth. The posterior transverse ridge formed by the bosses and notch rises half again as high above the triangular nape scales as they are tall and projects slightly backward above the small interval before the crest scales begin.

No parietal eye. The scale believed to be the interparietal identified on position and shape. It is in the midline anteriorly, a rather small, narrow triangle anteriorly in contact with the semicircles. Lateral to this scale are apparent parietal scales, the largest

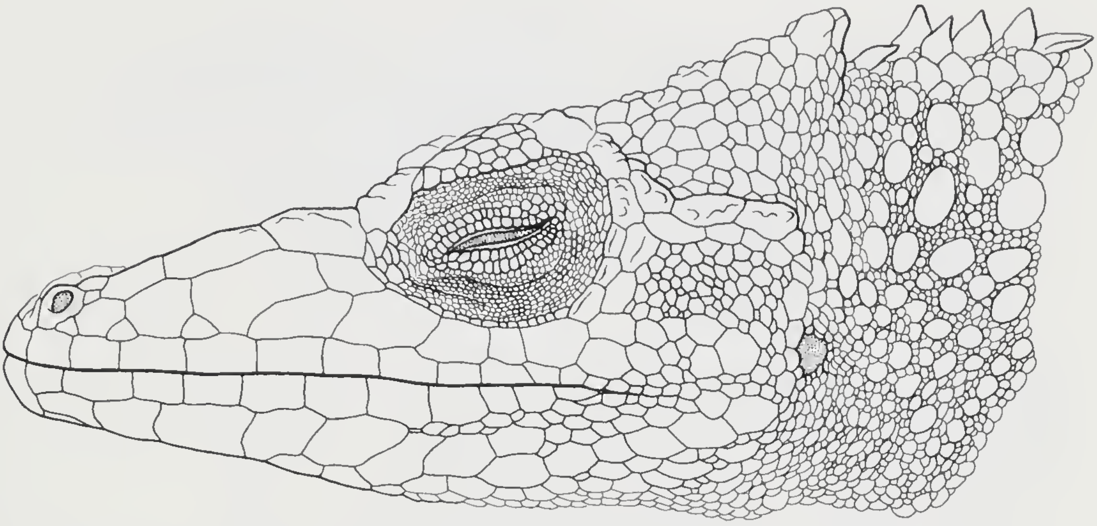


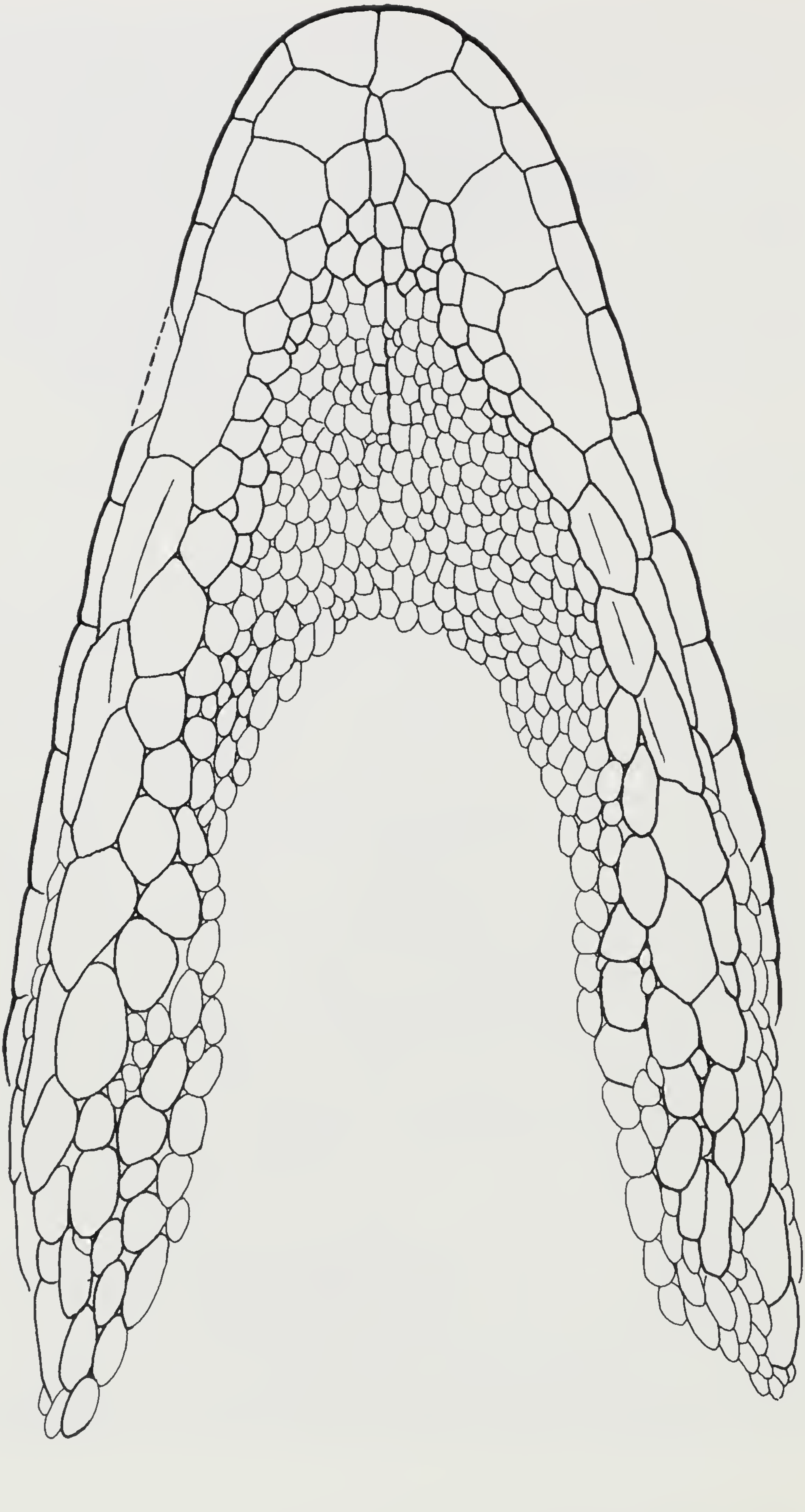
Figure 3. *Phenacosaurus vanzolinii* holotype, MECN 0309, Lateral view of head.

scales in the parietal area, subtrapezoidal, in contact with the semicircles, posteriorly meeting behind the median "interparietal." The scales further posterior irregular in size, shape, and arrangement. A count of about 6 to 7 scales from the "interparietal" to the notch at the posterior end of the casque.

Lateral head scales (Fig. 3)—All scales on lateral surfaces of head smooth, except the canthals, which are rugose and pustulate. Loreals in two rows, either the upper or the lower row interrupted. On right side, 5 large, 1 small scale in lower row, 1 large and 1 small in upper row, total 8; on the left side, one large, 3 small in lower row, 3 large in upper row, total 7.

Preoculars 2 right side, uppermost in contact with second canthal, 1 left side, in contact with second canthal. Suboculars 4 on each side, broadly in contact with supralabials. Postoculars in double rows, 5 in each anterior row, larger than adjacent temporals, 3 in each posterior row, which meets the intertemporal bar.

The upper temporals variable in size, small to subgranular. An intertemporal bar abruptly projecting, shelf-like, covered by only 3 large scales, but 1 row of smaller scales above and 1 below on the base of the ridge. Lower temporals exhibiting 2 regions, the upper with smaller scales than the lower except that there are irregular small scales around the corner of the mouth. Supralabials



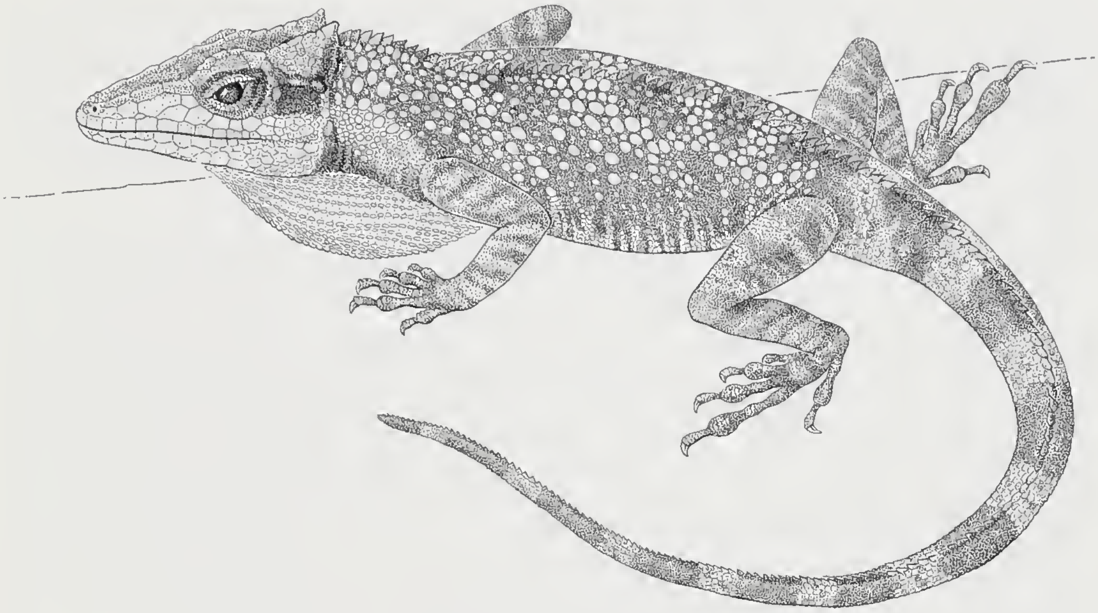


Figure 5. *Phenacosaurus vanzolinii,* holotype, MECN 0309, Lateral view of entire animal.

elongate rectangles, 8–9 on both sides to below the center of the eye.

Ventral head scales (Fig. 4)—Mental partly divided, deep, subpentagonal, not indented, in contact with 3 scales between the infralabials. Nine infralabials on right side, 10 on left. Very large first sublabials, each more than 5 × the size of the single median gular. Three somewhat smaller sublabials on each side, in series with the first, in contact with the infralabials. Total sublabials on each side five. Central gulars smooth, swollen, variable in size, largest adjacent to the sublabials. Posterolaterally, posterior to the sublabials, the lateral gulars mostly much enlarged, but very variable in size, in several distinct rows.

Dewlap (Fig. 5): Edge scales convex, smooth, smaller than ventrals. Lateral scales about the same size as the edge scales, in single rows separated by naked wrinkled skin.

←

Figure 4. *Phenacosaurus vanzolinii,* holotype, MECN 0309, Ventral view of head.

Trunk (Fig. 5): Dorsal crest of triangular scales, beginning on the nape 2 small scales behind the abruptly vertical casque, high anteriorly, only low above the sacrum. Nearly continuous in a single row, interrupted at irregular intervals by median contact of the paravertebrals.

Flank scales very heterogeneous, with at least 3 classes of scales: (1) prominent very large round flat scales, (2) smaller round flat scales, no more than ¼ the size of the largest, (3) small convex scales and granules as well as naked skin. The largest scales on the lower flanks. The paravertebrals, which belong to the first class of very large scales, in 1 or 2 rows, posteriorly in contact or slightly imbricating, anteriorly always separated by granules or naked skin. Other very large scales always separated by the other 2 classes of scales, separated most widely on lower flanks.

Axilla and groin granular. Ventrals smaller than the largest flank scales, averaging a little larger than the second class of flank scales, rather irregular in size and shape, imbricate or subimbricate.

Limbs (Fig. 5): Anterior face of forelimbs mostly with separated flat smooth scales. Anterior face of hindlimb mostly with scales in contact. Posterior face of upper arm and thigh with granules separated or in contact, of lower arm and leg with small scales mostly in contact. Supradigitals smooth. Subdigitals all lamellar. Lamellae under phalanges ii and iii of fourth toe 25–26.

Tail (Fig. 5): Strongly compressed, with a crest of larger sharply keeled, dentate scales. All scales keeled except a few rows above at the base of the tail and about 8 rows immediately behind vent. Postanals much enlarged (male).

Color in life: No descriptions of the color in life of the type series exist. Fortunately, we do have slides of the holotype. It is revealed to be dorsally greenish in background with the underparts totally white. The large round scales are often yellow or lighter green. There is some vague tendency to banding. The head scales have an orangish cast when not overlaid by green smudging. A broad white band unites the supralabials. There is yellow banding on the limbs and digits.

Variation: The Adult Paratypes. Head: The casque is high to very high posteriorly and its lateral crests are always significantly raised above the central parietal roof.

Dorsal head scales—Antorbital area: Pustulations may extend far forward but never to the tip of the snout or the area between the circumnasals. Small scales may extend only alongside the fourth (anteriormost) canthal or reach the anterior end of the third as in the holotype. There are 3 postrostrals in EPN 2221 and 4 in all others. The rostral area is injured in 3 specimens (EPN 2219, MCZ 175160, and USNM 293683), in all the circumnasals appear to be, as in the holotype, narrowly in contact with the first supralabial, and separated on each side from the rostral by one of the frontal depression there is always a rosette of scales surrounding a central scale or scales, but in EPN 2221 the central scale is relatively large and there is a small scale off center to the left. In EPN 2219, MCZ 175160, and USNM 293683 there are 2 small or moderate scales at the center of the rosette. In MCZ 175159 there are 2 rosettes, the posterior with a small scale, the anterior with a large scale in center but a small scale just off center. The large scales of the rosette may be pustulate or with none or few pustules.

The canthals are always 4 and the anteriormost always separated from the circumnasals by at least 2 superimposed scales. The third is always largest and expanded medially. The first canthal may or may not be expanded medially. These scales are nearly smooth in MCZ 175159, except for a few pustulations, but more or less wrinkled in the other paratypes, which are more or less heavily pustulate as well.

Orbital area: The scales of the semicircles are always pustulate to heavily pustulate except the extreme posterolateral scales, which may entirely lack pustules. The supraoculars, on the other hand, and the superciliaries, are always smooth or very finely shagreened. A single pair of the scales of the semicircles may meet medially or these may be wholly separated by 1 row of rather large pustulate scales. The supraoculars are relatively few in number, the enlarged scales in 2 or 3 rows, with the largest scales medial and in contact with the semicircles, and one or more of the lateral enlarged scales in contact with the superciliaries. A few smaller scales, variable in size and number, fill the remainder of the supraocular area. The anteriormost 1 or 2 of the superciliaries in all of the type series fully exposed dorsally, larger, and subtriangular or subtrapezoidal. The remainder of the single row of superciliaries is quadrate, subequal or the posteriormost again larger, and in 5 of 6 specimens barely exposed dorsally, mostly on the lateral surface of the head. In MCZ 175160, the entire row is fully exposed dorsally, and the anteriormost element best described as quadrate like the other superciliaries.

Parietal area: These scales in the paratypes are extraordinarily variable, not only in size and shape but also in rugosity and pustulation. EPN 2219 shows an extreme in pustulation with very little rugosity; MCZ 175160, on the contrary, is extreme in rugosity, which nearly conceals all pustulation.

The lateral crests, as in the holotype, slope upward toward posterior bosses that, however, are either the lateral borders of a more or less deep notch or of a transverse occipital ridge. A notch like that of the holotype occurs only in EPN 2219. In USNM 293683 and EPN 2221, a series of 4 bosses unite to form a transverse ridge. In MCZ 175160 and MCZ 175159, there are 4 transversely oriented bosses but a narrow and deep notch.

No parietal eye in any adult specimen. In EPN 2221 and MCZ 175160, a smaller and shorter scale occurs in the position of the "interparietal" of the holotype, but the scales called "parietals" in the holotype are broken up in both specimens. In the 3 remaining adult paratypes, the scales are so irregular or asymmetric that no interparietal is plausibly demonstrable. In consequence, counts from interparietal to the posterior crest of the casque can only be made in EPN 2221 (4 or 5) and MCZ 175160 (6 or 7).

Lateral head scales—All lateral scales are smooth in the paratypes except USNM 293683, which has the canthals pustulate as in the holotype. Only MCZ 175160 has a single loreal row on both sides. The total number of loreals in this specimen is 4 or 5, the series grading in size anteriorly. On both sides the very large and long preocular has a dorsal vertical groove at the middle of its length, indicating that 1 loreal has fused with the preocular on each side. If so, the true total count of loreals would be 5 and 6, respectively. The other paratypes have 2 rows, 1 row, upper or lower, always interrupted. The total number of loreals in these paratypes varies from 7 to 9. Preoculars are 2 in 3 of the paratypes as in the holotype. In EPN 2219 and 2221, however, there is only 1 preocular on each side. In all cases, the preocular is in contact with the second canthal. The suboculars vary from 3 to 4 in 4 paratypes and are 5 only on one side of EPN 2219. Postoculars are in 2 rows behind the eye (on the bony ridge that is the junction of jugal and postorbital). The number of postoculars in each row varies from 3 to 5; only in MCZ 175159 does the number of postoculars rise to 6 in each of the 2 rows on the right side and to 6 on the posterior row, 7 in the anterior row on the left. The supralabials are elongate rectangles in all specimens, and the number to the center of the eye varies from 7 to 10.

The temporal area is in all specimens divided into supra- and infratemporals by a very prominent projecting, shelf-like intertemporal ridge (marking externally the squamosal–postorbital bar that is the lower border of the upper temporal fenestra). The edge of the intertemporal ridge is covered by 2 large horizontally extended scales in all paratypes. The number of scale rows entering the ridge base from the supratemporals or infratemporals varies from 0 to 1 on the upper or lower side independently.

The supra- and infratemporals are quite smooth. Where in the supratemporal region a scale overlaps the edge of the casque, the scale is always smooth on the supratemporal side, always wrinkled, rugose or pustulate on the parietal side. Most of the supratemporals are subequal and polygonal, but occasional smaller polygonal or narrow scales intervene posteriorly. The infratemporals divide abruptly into 2 regions differing in the size of their scales. The abrupt size difference is coincident with the margin between dark and light pigment in this lower temporal region. This condition is consistent in all the paratypes as well as in the holotype, but in the paratypes as in the holotype, just below the intertemporal ridge larger scales again occur, and at the lower margin around the corner of the mouth quite small scales are found.

Ventral head scales—The mental is always semidivided. It varies somewhat in width but is always as deep as it is wide, and not or only slightly indented by the sublabials or medial gulars. The first sublabials vary much in size and may be significantly different in size on the 2 sides of the same animal. However, they are always at least 4–5 × as large as the medial gulars that lie between them, although these also vary very much in size. The first sublabials are in series with a row of sublabials, each of which may be as large or larger than the first. A total of 4–7, always counting the first, may be in contact with the infralabials. The central gulars, those that cover the throat posterior to the medial gulars that lie between the sublabials, are always smooth, mostly juxtaposed, swollen, elongate, and larger anteriorly, becoming smaller and more rounded, subimbricate in the center of the throat. Granules are visible between some of the central gulars. Those gulars that lie next to the sublabials are consistently larger than those occurring centrally.

Lateral to and behind the sublabials and lateral to the insertion of the dewlap are lateral gulars. The anterior ones are tiny, barely separating the sublabials from the infralabials. These become larger posteriorly and, indeed, become as large as the posterior sublabials from which they are distinguished by their orientation.

Dewlap (all paratypes are males): Moderate, not extending posteriorly much beyond the insertion of the arms. Edge scales, smooth, imbricate, smaller than ventrals. Lateral scales, about the same size as edge scales, in very regular single rows, the scales well separated by wrinkled skin or by wrinkled skin with very occasional minute scales.

Trunk: A dorsal crest of a single row of triangular interrupted at irregular intervals by 2 paravertebral scales joining across the midline, highest on the nape, lowest on sacrum.

There are 3 classes of flank scales: (1) round, flat scales, varying in size but larger than crest scales; (2) round, flat scales much smaller than class 1 (¼ their size or less; (3) convex granules, large or small, some almost as large as some class 2. One or more rows of paravertebrals of class 1 size are always in contact or separated by only 1 row of class 3 granules or scales. Class 1 scales lower on the flank, on the other hand, are always separated by 2–5 rows that include class 2 scales and/or smaller class 3 scales or granules.

The ventrals are always smooth, flat or slightly convex, imbricate and about the size of class 2 scales or slightly larger.

Limbs: Anterior upper arm scales smooth, variable in size, sometimes imbricate. Posterior upper arm scales granular, juxtaposed.

Anterior lower arm scales smaller, narrower, smooth, subimbricate. Posterior lower arm scales granular, juxtaposed.

Manus with weakly multicarinate scales, imbricate dorsally on carpus, palm scales narrower, subimbricate. Supradigitals multicarinate. All subdigitals lamellar.

Thigh scales anteriorly large, smooth, subimbricate proximally, imbricate at knee, posteriorly with narrow scales, subimbricate or juxtaposed. Tibial scales smooth, small, narrow and imbricate anteriorly, subgranular and subimbricate posteriorly. In EPN 2219, larger scales are found among the granules.

Pes with scales dorsally and on the sole indistinctly carinate and subimbricate. Supradigitals weakly multicarinate. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 24–28.

Tail: Always strongly compressed and with a distinct crest of keeled scales, which, however, varies in height but, in most paratypes, has a dentate appearance. The lateral caudal scales are always keeled, except dorsally at the base and ventrally for 5–10 rows behind the vent.

Variation: The Juvenile Paratype. The juvenile EPN 2218 requires a separate description. Many of the differences are surely ontogenetic, but it is not obvious that all of them are. Differences between this specimen and the remainder of the type series are italicized.

Head: There is no casque but its margins are partially indicated by low ridges (lateral parietal crests) bounding the parietal area.

Dorsal head scales—Antorbital area. *There are no pustulations.* Scales at the tip of the snout and 2–3 rows posterior to the circumnasals and a few scales between the canthals and a larger median row of scales are small. A total of 7 postrostrals, 5 almost granular postrostrals in addition to the larger circumnasals. Each circumnasal is broadly in contact with the first supralabial of its side. There are 3 small scales between the circumnasals dorsally.

The frontal depression is very shallow with large scales forming a rosette around small scales in the center.

The canthals are *6 on the left side,* 5 on the left, gently arched, not keeled, the first (posteriormost) widened medially on both sides, third largest, also expanded medially, *the anteriormost on the left side in contact with the circumnasal, that on the right separated from the circumnasal by 1 small scale.*

Orbital area: The supraorbital semicircles are separated medially by a single row of scales only slightly smaller than those of the semicircles. One especially large supraocular in contact with the semicircles on each side. Two to 3 enlarged supraoculars in a second row, not in contact with the superciliaries. Other scales of the supraocular region smaller. Two or 3 short polygonal anterior superciliaries followed by quadrate subgranular scales.

Parietal area: A parietal eye indicated by a light spot in the hexagonal interparietal, the largest scale in the parietal area and separated from the semicircles by a large scale on the left side and by 2 small scales in a row on the right side.

There are moderate-sized scales that abut laterally on the interparietal but they do not meet behind it and intervening scales of small or moderate size separate these from the semicircles as well as others that separate them from scales that cover the lateral parietal crests and are larger than any scales of the parietal area except the interparietal.

The lateral parietal crests converge but do not meet. There is, instead, a wide gently convex medial area, presumably marking the position of the future posterolateral bosses and the median notch. Over this gentle convexity, 4 rows of small scales, here called "notch scales," precisely comparable in size to the nape scales, enter the parietal area to abut against the 4–5 rows of abruptly larger (moderate-sized) scales behind the interparietal.

Lateral head scales—Two loreal rows, 8–10 total loreals, 4 large and 4 small on the right side, 4 large and 6 small on the left side.

Preoculars 2, counting on each side the upper scale that overlaps the loreal rows and excludes the lower preocular from contact with the second canthal. Five suboculars each side, broadly in contact with the supralabials. Eight to 10 supralabials to below the center of the eye.

Temporals smooth, flat. Lower temporals variable in size, but a vaguely indicated division by scale size with the scales averaging smaller in the upper pigmented region and larger in the lower unpigmented region. A well-defined intertemporal row beginning with a single large elongate scale and continuing as a double row of slightly enlarged scales. Upper scales subequal with an abrupt transition at the lateral parietal ridges where the enlarged scales of the parietal area begin.

Ventral head scales—Mental partly divided, in contact with 4 postmentals between the infralabials, 2 medial gulars between the very large first sublabials. Three additional sublabials in series with the first on each side are in contact with the infralabials.

Central gulars smooth, juxtaposed or subimbricate. Some of the posterior gulars next to the sublabials markedly enlarged, nearly as large as the last sublabial. Lateral gulars intervene between the posterior sublabials and the infralabials.

Trunk: A dorsal crest begins on the nape, seven scales behind the enlarged scales of the parietal area, as raised, still relatively small protuberant scales in 1 or 2 rows, rising to 3 broad-based triangular typically blade-like crest scales in sequence, behind which the crest is only indicated by a series of enlarged smooth oval scales, interrupted at intervals by paravertebrals joined over the midline. Flank scales heterogeneous with large round flat class 1 scales, largest dorsally and there often in contact, on lower flanks smaller and most often separated by class 2 and 3 scales and granules. Axilla and groin granular. Ventrals smooth, flat, irregular in size and shape, imbricate or subimbricate.

Limbs: Anterior face of fore- and hindlimbs with imbricate or subimbricate flat smooth scales. Posterior face of upper arm and thigh with granules, of lower arm and lower leg with small scales. Supradigitals smooth. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 25.

Tail: Compressed, without a crest or a continuous middorsal row, smooth or with an occasional hint of keeling dorsally, none below, but the latter scales more convex. Postanals much enlarged (male).

Dewlap: There is no trace of a dewlap.

Food. Stomach contents from MECN 0327 were examined by James Carpenter (then at the Museum of Comparative Zoology). He reported:

> At least four taxa are present in the sample as follows:
>
> Order Lepidoptera, family Geometridae—an intact larva ("looper" or "inchworm").
>
> Order Coleoptera, family Buprestidae—elytra (forewings).
>
> Order Hymenoptera, Halictidae, tribe Augoclorini—head capsule, thorax, wing, parts of legs.
>
> Order Homoptera, Cicadidae—most of the large fragments, including a head capsule.
>
> In addition there are a number of eggs. These could be from the cicada.

Ecology. The holotype was collected by Robert Bleiweiss. He here provides an expanded version of his field notes:

> Collected during the early afternoon along a road cut. The animal was moving slowly and deliberately down the stem of a large vine belonging to the family Gesneraceae that was overhanging the road bank along a forested section of the road.
>
> The weather was sunny and warm. It was probably between 1 and 2:30 in the afternoon. The collection site was a few minutes drive down from La Alegría near a stream gorge and on the shady side of the road.

Juan Carlos Matheus collected the second (damaged) specimen dead in the road near the same site.

Ana Almendáriz has reported on the times and sites of collection of the remaining specimens that have exact data. All were collected between 10:00 and 12:30 A.M., and all were collected along roads. The days of collection were humid, but at the moments of collection there was never rain but, instead, a bit of sun—"un poco de sol."

Ana Almendáriz has also provided a description of the general region where she collected (translated):

> While the region is within the 'cloud forest zone', it has been heavily cultivated, removing the trees that were of commercial value, then clearing the forest for field crops. Original forest is therefore confined to slopes and ravines difficult of access. The margins of the roads are covered with secondary vegetation, mostly Asteraceae.

She reported also that the local people say that the "camaleon o camelion" is common in the fields of maize. Bleiweiss and Matheus collected at La Alegría at higher elevations with steep terrain. This area, the type locality, was still heavily forested in 1985.

The ecology reflected by these experiences accord wells with the observations of Williams collecting *heterodermus* in the Sabana de Bogota and with the more extended observations made by Kenneth Miyata on 2 full days of study in August 1973 (Miyata, 1983).

Comparisons. Phenacosaurus vanzolinii requires comparison primarily with *P. inderenae.* The species are both giant, with *P. inderenae* significantly the larger, given the small series of both that are available. Both have rather similar coloration and both have highly differentiated flank scales—the three classes of scales described above—seen also in *P. heterodermus.* Both differ from *P. heterodermus* not only in size and the associated development of the casque but also in color pattern and details of squamation.

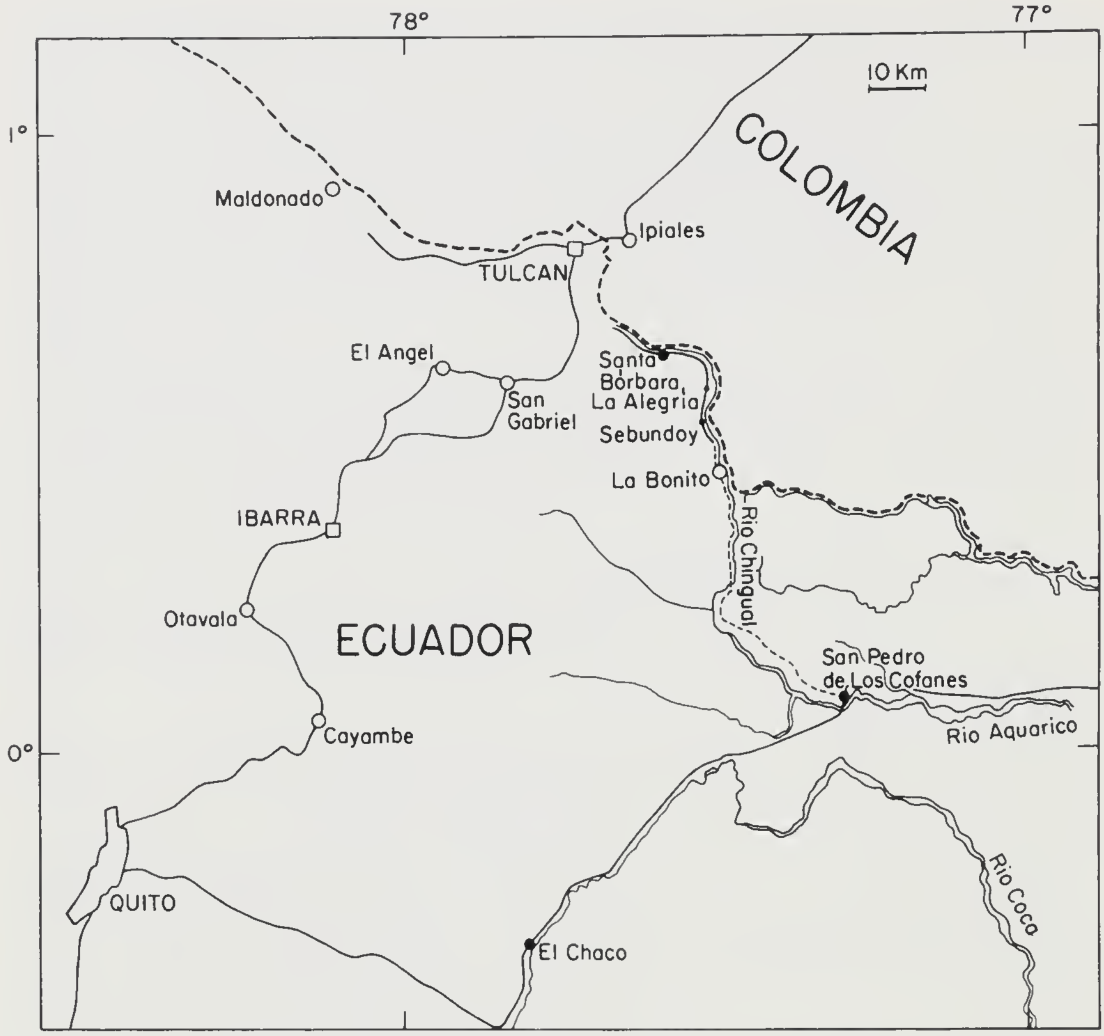
For the comparison of the two giant species, we have available the whole of the type series of *P. inderenae,* three females and one male, generously loaned by Hernández–Camacho and Rueda. For better comparison, we describe these specimens in the same detail as we have previously done for the type series of *P. vanzolinii*: one female, Inderena (IND)-R 2999, has already been quite accurately illustrated (fig. 1 in Rueda and Hernández–Camacho, 1988). The single male, IND-R 3381, is illustrated in our Figures 6–9.

Head: The head is casqued as massively and the posterolateral bosses of the casque are about as high as in any *P. vanzolinii.*

Dorsal head scales (Fig. 7)—Antorbital area: There appear to be larger scales behind the circumnasals and between the canthals and the median larger scales and no small scales in the frontal depression. The scales between the circumnasals appear to be larger than in *P. vanzolinii.* Postrostrals vary from 3 to 5, 3 in the holotype female IND-R 3213, 4 in IND-R 3744 and 3381, and 5 in IND-R 2999, in the latter case including the circumnasals, which are in broad contact with the first supralabials but only narrowly in contact with the rostral. In the 3 other specimens, the circumnasals are again broadly in contact with the first supralabials but separated on each side from the rostral by one of the postrostrals.

In the frontal depression in all specimens the scales are smooth and large. There is no rosette surrounding a central small scale. Instead, there is a symmetrical arrangement of 4 large scales, 1:2:1, and there are always 2 scales (3 or 4 scales in *vanzolinii*) between the second canthals across the frontal depression.

The canthals are smooth or very bluntly keeled. There are 4 asymmetrically in IND-R 2999, 4 left side, 5 right side, or 5 in all the others. On both sides of all specimens the anteriormost canthal is in contact with the circumnasals (separated by 2 superimposed small scales in *vanzolinii*).


78°
77°
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10 Km
COLOMBIA
ECUADOR
Maldonado
Ipiales
TULCAN
El Angel
San Gabriel
Santa Bárbara,
La Alegria
Sebundoy
La Bonito
Rio Chingual
IBARRA
Otavalo
San Pedro de Los Cofanes
Rio Aguarico
Cayambe
Rio Coca
QUITO
El Chaco

Figure 6. The known localities for *P. vanzolinii.*

Orbital area: In all 4 *inderenae,* the scales of the semicircles are wrinkled and vary from not to moderately pustulate, with 2 or 3 pairs in contact medially (1 or none in *vanzolinii*). The supraoculars (as in *vanzolinii*) are smooth or very finely shagreened. On both sides of all specimens the 2–3 largest scales are in contact with the semicircles, the 4 scales in the second row are in contact with the superciliaries, and a central scale is interposed between the first and second rows. As in 2 of the 6 paratypes of *P. van-*

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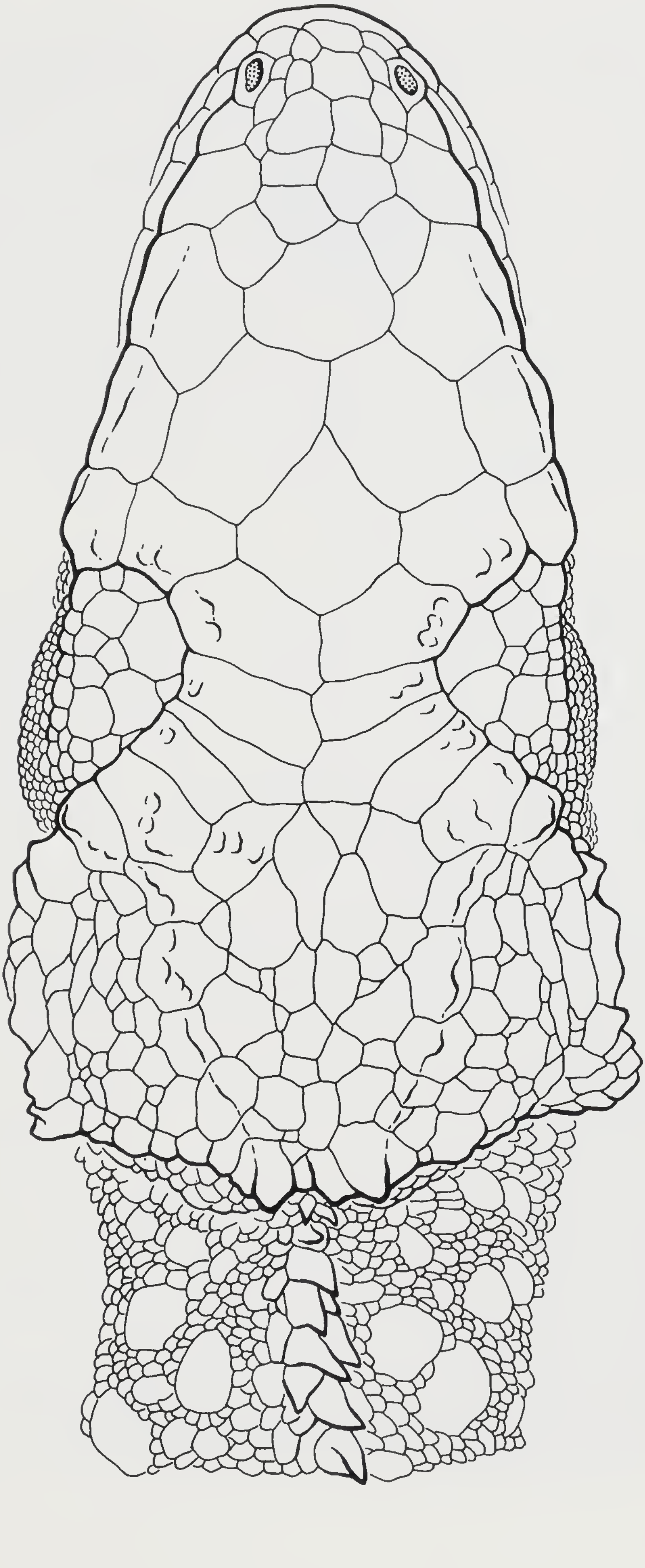
Figure 7. *Phenacosaurus inderenae,* paratype male, IND-R 3381, Dorsal view of head.



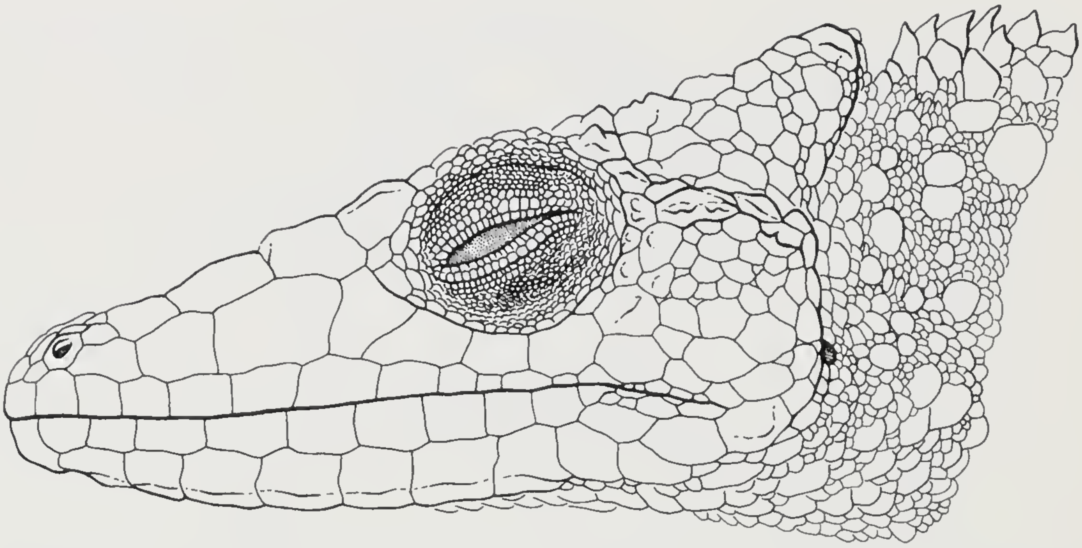


Figure 8. *P. inderenae,* paratype male, IND-R 3381, Lateral view of head.

zolinii, the superciliaries in IND-R 3381 and IND-R 2999 are fully exposed dorsally. In the holotype, the largest specimen, and IND-R 3744, the smallest, only the 2 or 3 largest superciliaries are visible dorsally, but in both of these the eyes are somewhat sunken in, and this feature may be an artifact. As in *vanzolinii,* the first superciliary on each side is larger and trapezoidal, and there are about 7–8 subequal posterior superciliaries.

Parietal area: There is no parietal eye in any specimen. In contrast to *vanzolinii,* there is a recognizable interparietal in all cases, diamond-shaped, variable in size, in narrow contact with at least 1 of the 2 scales of the last conjoined pair of the semicircles. Two pairs of scales lateral to the inferred interparietal are always relatively large and regular but not always symmetrical in shape or size. However, the posterolateral pair does not meet behind the interparietal. Instead, in all specimens 1 or 2 smaller scales, narrow and triangular, intervene posteriorly. The lateral crest scales are wrinkled and slope rather gently upward (more steeply in the male IND-R 3381) posteriorly toward the posterolateral bosses, which are separated by a notch, deep in the male, shallower in the females. Five to 7 scales can be counted from the interparietal to and including a notch scale.

Lateral head scales (Fig. 8)—As in *vanzolinii,* all the lateral head scales, other than the canthals, are smooth. The canthals may be weakly rugose but are never pustulate (as in some *van-*

zolinii). The loreals are in all specimens in only 1 row (usually 2 rows in *vanzolinii,* but 1 row on both sides in USNM 293683). The total number of loreals varies from 3 to 5 (7 to 9 in *vanzolinii*) (5 on both sides in the holotype of *inderenae*; 5 on the left side, 4 on the right in IND-R 3381; 4 on the left side, 3 on the right in IND-R 2999; 3 on both sides in IND-R 3744). There is one very large preocular in series with the loreals and in contact with the second canthal. There are 3 or 4 suboculars, 4 on both sides in the holotype of *inderenae,* 4 on the left side in IND-R 33821 (3–5 in *vanzolinii*), all broadly in contact with the supralabials. The postoculars are in 2 rows, 5 in the anterior row, 2 in the posterior row, the latter large scales that dorsally are in contact with the intertemporal ridge. The supralabials are 6 or 7 to below the center of the eye (7–10 in *vanzolinii*).

The intemporal ridge is distinctly shelf-like in *inderenae* but less regular than in *vanzolinii,* varying in shape and squamation.

The supratemporals are moderate, subequal, except on the posterolateral edge of the casque where they are smaller, narrower and vertically elongate.

The infratemporals tend to be smaller in the pigmented area of the infratemporal region and are distinctly smaller ventrally at the corner of the mouth. However, the distinction between the 2 zones of infratemporals—a smaller upper pigmented zone and a larger lower unpigmented zone—is decidedly blurred in *inderenae* as compared with the sharp distinction seen in *vanzolinii.*

Ventral head scales (Fig. 9)—The mental is wider than deep, almost completely divided (semidivided in *vanzolinii*), and indented posteromedially (not or only slightly indented in *vanzolinii*). The first sublabials vary as much or more in size as in *vanzolinii* and, again as in *vanzolinii,* may vary impressively on the 2 sides of 1 animal. In a unique instance (IND-R 2999), the left median gular (a gular in contact with the mental) is more than ¼ the size of the left first sublabial. In all other cases in both species, despite the striking variation in sublabial size the first sublabials (and most of the succeeding sublabials) are much more to very much more than 4 × the size of any median gulars.

The number of sublabials in contact with the infralabials compared for *inderenae* and *vanzolinii,* shown in Table 1, barely overlaps.

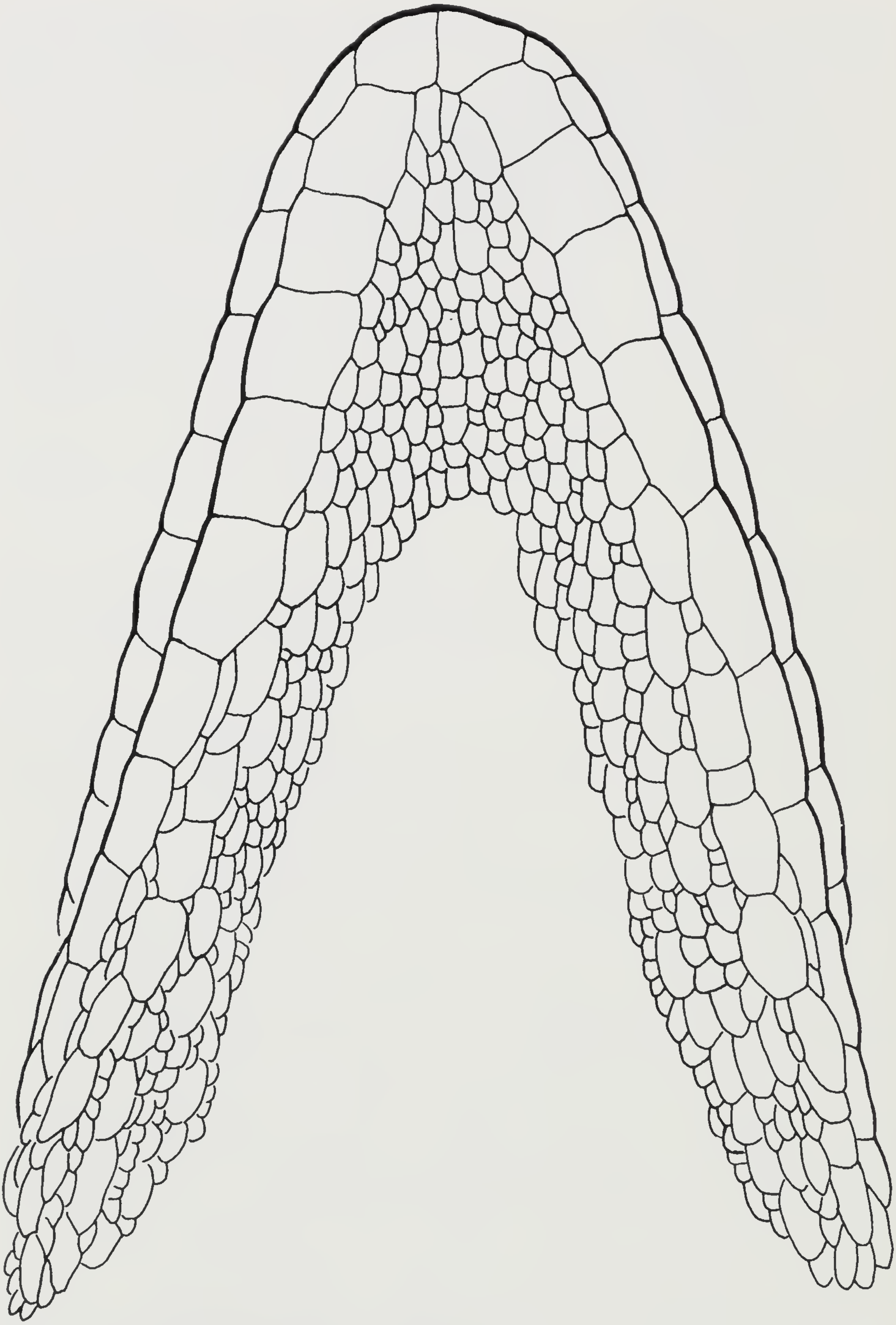


Figure 9. *P. inderenae,* paratype male, IND-R 3381, Ventral view of the head.

TABLE 1. SUBLABIALS IN CONTACT WITH INFRALABIALS.

Inderenae		Vanzolinii	
2999	8/6	2221	6/7
3381	8/7	175160	4/4
3744	7/8	2219	5/4
3213	7/9	309	5/5
		293683	5/6
		2220	5/6

The lateral gulars of *inderenae* are much like those of *vanzolinii,* tiny anteriorly between the sublabials and infralabials, larger to much larger behind the sublabials, from which, as in *vanzolinii,* they are distinguished by orientation. However, while in *vanzolinii* the lateral gulars may be large to quite large as they approach the insertion of the dewlap, the similar scales of *inderenae* are of 2 sizes only, moderate and small, well intermixed.

Dewlap (Fig. 10): As in *vanzolinii,* the dewlap of *inderenae* is moderate, not reaching much beyond the level of the insertion of the arms. There appears to be no appreciable sexual difference in this character, the dewlap of the single male of *inderenae* known, IND-R 3381, extending little or no farther back than that of the 3 females. The scales of the edge are smooth, imbricate, smaller than ventrals in both sexes. The lateral scales, while in rows, are, unlike *vanzolinii,* not separated by wrinkled naked skin but by numerous small scales, variable in size with larger scales next to the row scales, often making it difficult to determine whether the rows are single, double, or indeed multiple. Some rows are incomplete.

Trunk (Fig. 10): There is a single dorsal crest as in *vanzolinii* and, as in *vanzolinii,* it is interrupted at irregular intervals by 2 paravertebral scales that abut across the midline. As in *vanzolinii,* it is highest on the nape. There are 3 classes of flank scales as in *vanzolinii* and *heterodermus.* However, unlike the other two species, the class 1 scales are often more than twice as high and wide as the crest scales are high.

Ventrals in *inderenae* are smooth and imbricate, as in all phenacosaurs, but in this species substantially larger than class 2 flank scales.

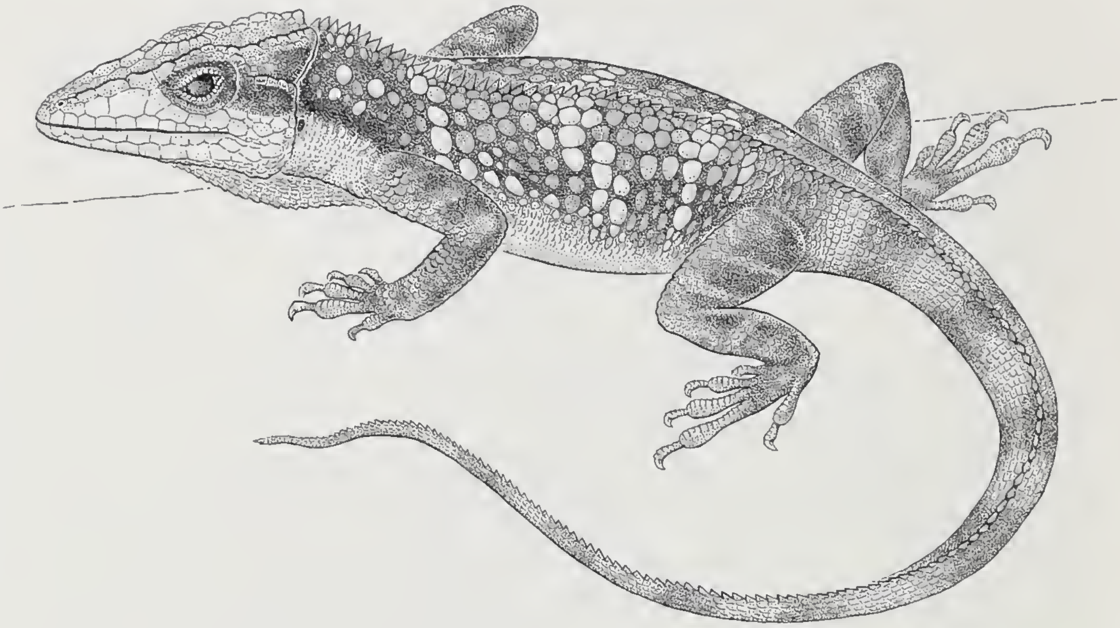


Figure 10. *P. inderenae,* paratype male, IND-R 3381, Lateral view of entire animal.

Limbs (Fig. 10): Anterior upper arm scales smooth, strongly imbricate to subimbricate, some larger than ventrals. Posterior upper arm scales granular, separated.

Anterior lower arm scales smooth, variable in size, smooth, subimbricate. Posterior lower arm scales granular subimbricate.

Manus with smooth scales, imbricate dorsally and on palm. Supradigitals smooth, all subdigitals lamellar.

Thigh scales anteriorly smooth, not as large as some upper arm scales, about as large as ventrals, imbricate proximally, subimbricate at knee, posteriorly smooth, swollen, smaller but variable in size, partly imbricate, partly separated. Tibial scales smooth, imbricate to subimbricate.

Pes with supradigitals smooth or very weakly carinate. All subdigitals lamellar. Lamellae under phalanges ii and iii of fourth toe 23–31.

Tail (Fig. 10): Strongly compressed with a dentate crest. Distal caudals keeled.

Color in life: There is an elaborate description of the color in life of the holotype. Two slides of color in life also exhibit color change. There is also the slide of the Houston Zoo animal taken by Harry Greene. The impression is that of a dorsally red brown animal that can change the vague dorsal banding to black.

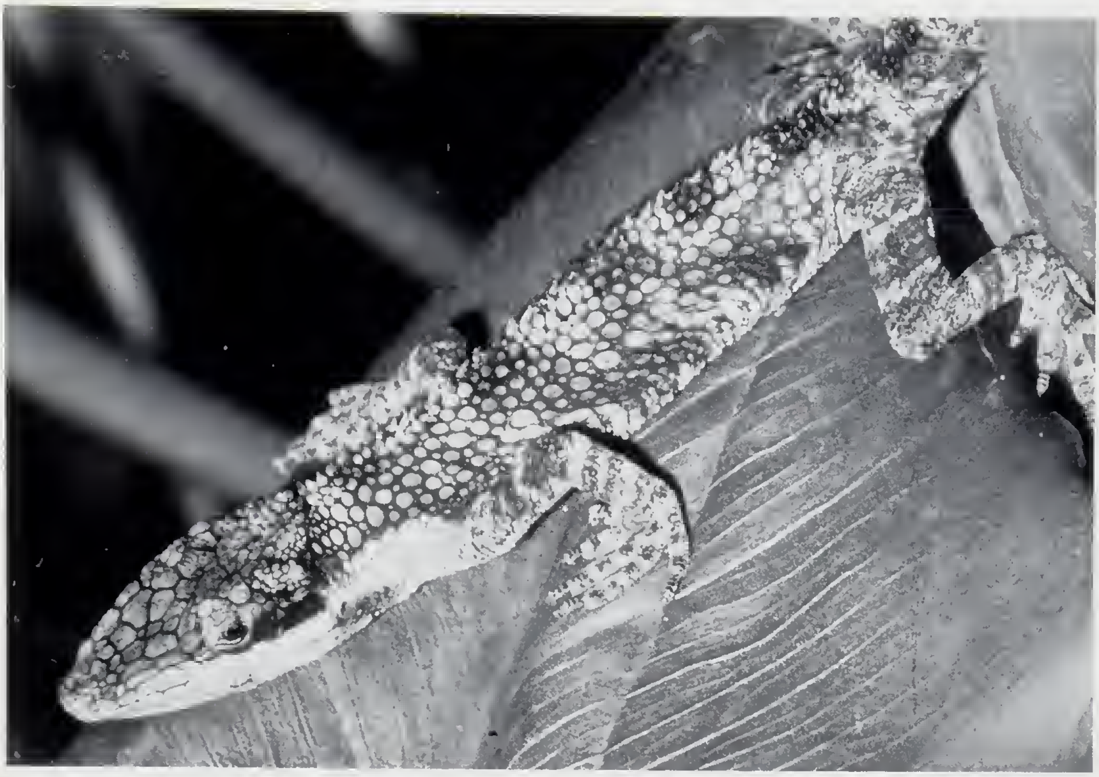


Figure 11. Photo in life of the holotype of *Phenacosaurus* vanzolinii. Robert Bleiweiss, photographer.

DISCUSSION

Comparative Ecology and Behavior

Only Hellmich (1949) of those who have seen *Phenacosaurus* in the field has even the appearance of considering the genus as limited to páramo. In his case, his characterization of *Phenacosaurus* as a "Paramo-echse" may refer only to the species, named from a single specimen, found on the ground among the Espeletia in the Páramo de Sumapaz (a páramo that overlaps the borders of Cundinamarca, Meta, and Huila). He was, as appears from the text of his discussion, quite aware of the considerable range of elevations and habitats in which the genus has been found. Although, on the evidence of Hellmich's single specimen, the genus is found in typical páramo, it is, in fact, known from a surprisingly broad range of elevations below those that support páramo under natural conditions.

All specimens of *P. vanzolinii,* for example, were collected between 1,950 and 2,630 m. These elevations, all on the eastern

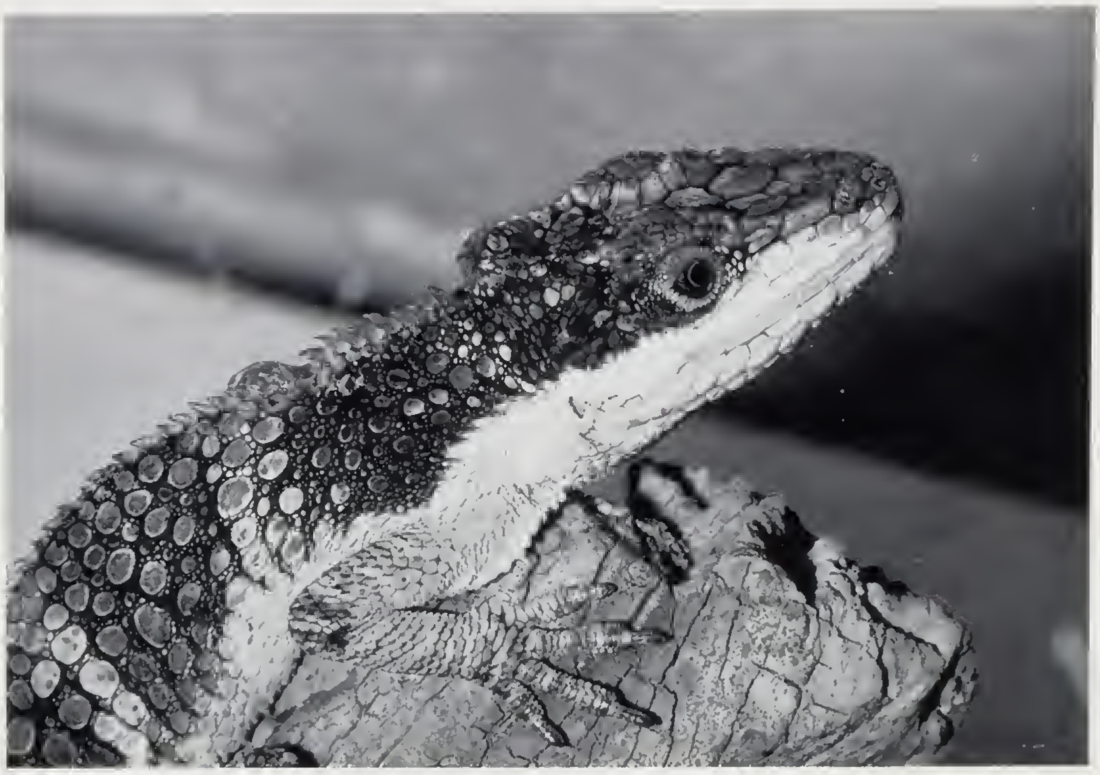


Figure 12. Photo in life of the no locality *Phenacosaurus inderenae.* Harry Greene, photographer.

slope of the Andes, are in the forested zones corresponding to the humid premontane and montane formations of Holdridge (1967). The forests are typically tall and often bathed in clouds for much of the day. The trees, including many tree ferns, are heavily laden with epiphytes and mosses. Although human activities have destroyed much of the natural forest vegetation along the road between Santa Bárbara and La Bonita, large patches still exist along the steep slopes above the road and in the steeper stream gorges.

The scanty data from Bleiweiss's and Almendáriz's field notes are surprisingly consistent on a number of points. Bleiweiss collected the type on a sunny afternoon around 1:00 P.M., after the clouds had lifted: "The animal was moving slowly and deliberately down the stem of an unidentified (herbaceous) Gesneraceae overhanging the [upper] bank along a forested section of the road." Similarly, Ana Almendáriz reported that her specimens were collected along roads between 10:00 and 12:30 A.M. in humid but sunny weather.

These observations are congruent with those of a group led by Williams that collected *P. heterodermus* north of Bogota and with Miyata's (1983) more detailed account of the same species in the same area. It may well be characteristic of *P. vanzolinii* and its close relatives of the *heterodermus* species group within *Phenacosaurus* to be most active at midday and/or in relatively sunny weather.

Zoogeography

Robert Bleiweiss

The discovery of a new species of *Phenacosaurus* is not surprising given that the remarkably diverse Andean herpetofauna remains poorly known (Lynch, 1986). We are nevertheless impressed by its discovery in the Santa Bárbara region. There is nothing about the physical relief or general climate of this section of the Andes to suggest that it might harbor endemic lizard species. Moreover, a large collection of forest frogs made by Bleiweiss and Matheus at the same time that they obtained the new *Phenacosaurus,* although containing new *Eleutherodactylus* and *Colostethus* species, appears no more distinctive than similar collections from other high-elevation sites in the northern Andes (W. R. Heyer, personal communication).

The discovery is, in fact, interesting primarily in showing how little we know about the Andean herpetofauna. The original impetus for Bleiweiss's exploration of the Santa Bárbara area was provided by his previous studies of geographic variation in the Andean hummingbird *Helianthus exortis,* a common resident of humid montane forests throughout Colombia and eastern Ecuador. The highly variable female plumage of *H. exortis* resolves into a striking dimorphism of male-like and female-like individuals in southern Colombia and northernmost Ecuador around Santa Bárbara (Bleiweiss, 1985a,b, 1991). Thus, avian patterns already suggest that the Santa Bárbara fauna was distinctive and had some zoogeographic connection with southern Colombia. In the absence of data from other vertebrate groups, birds provide the only available context for evaluating the new giant phenacosaur.

Indeed, several characteristics of Santa Bárbara's avifauna are noteworthy and parallel what is obtained in *Phenacosaurus.* A number of sources indicate that the avifauna is a mix of northern, southern, and even more typically western (Pacific slope) elements. Van Sneidern's recent collection of birds from the Andes of extreme southern Colombia, near the border between Putumayo and Nariño (0°31′N, 0°49′N), and thus close to Santa Bárbara (0°23′N), documented northern range extensions for seven species (Fitzpatrick and Willard, 1982). All were previously known no farther north than the Napo drainage in Ecuador (about 0°20′S) (Meyer de Schauensee, 1971). Moreover, Bleiweiss and Matheus (in preparation) collected two White-faced Nunbirds (*Hapiloptila castanea*), the first east slope records for a species known previously only from scattered localities on the Pacific slope. Bleiweiss and Matheus's own observations also indicate that at least two rare birds endemic to the east slope were actually common around Santa Bárbara and La Alegría, the Collared Jay (*Cyanolyca viridicyana*) and Red-hooded Tanager (*Piranga rubriceps*), which appears true also for their populations just across the Colombian frontier in Nariño (Hilty and Brown, 1986). The phenacosaurs show the same ecological phenomena: The sympatric occurrence in the Santa Bárbara area (at La Bonita) of a northern (*heterodermus*—see earlier) and one from a southern (*orcesi*) species group of *Phenacosaurus* suggests a faunal mixing zone.

Admittedly, these patterns are inferred from few data and can only be regarded as provisional. They do, however, suggest that future collecting along this poorly known section of the Andes will prove fruitful. One distinctive feature of the Eastern Cordillera of the Andes south from Bogota to around Santa Bárbara may bear on the patterns described earlier. Nowhere along this stretch are there peaks higher than 3,000 m (Vuilleumier, 1970). If high-elevation habitats are too limited in extent to support viable populations, then animals found just below in the forested zones may enjoy ecological release (Terborgh and Weske, 1975). This could explain this unusual mix and greater abundances of species along this segment.

The significance of the new *Phenacosaurus* for our understanding of Andean speciation patterns must await further phylogenetic studies. Present evidence cannot distinguish whether the taxon is a recently derived species or a relictual population of a once more widespread taxon. It is worth noting the Puffbird population of the Santa Bárbara region is morphologically distinguishable from populations on the Pacific slope (Bleiweiss and Matheus, unpublished observations). The possibility therefore remains that the lizard and the bird have differentiated in situ. This unprepossessing section of the Andes may turn out to be an ecological and evolutionary "hot spot."

ACKNOWLEDGMENTS

We are specially indebted to Ana Almendáriz and Alicia Arias for collecting five of the type series of *P. vanzolinii* and to Janira Regelado for providing two additional specimens. Without these specimens, the description of *Phenacosaurus vanzolinii* would have been extremely difficult or impossible. Without the drawings provided by Laszlo Meszoly, comprehension of the text would have been equally difficult or impossible. Brigitte Poulin assisted in proofreading the text. Publication costs were covered in part by a grant from the Wetmore-Colles Fund.

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A PHENACOSAUR FROM CHIMANTÁ TEPUI, VENEZUELA

ERNEST E. WILLIAMS,[1] MARIA JOSÉ PRADERIO,[2]
AND STEFAN GORZULA[3]

ABSTRACT. A new species of the genus *Phenacosaurus* is described from Chimantá Tepui, close to *P. neblininus.* It differs from *P. neblininus* (and other known phenacosaurs) in having the interparietal smaller than the ear and in having the circumnasal in broad contact with the rostral and only barely touching or not all in contact with the first supralabial. It also differs from *neblininus* in a generally darker coloration and having the belly with bold dark reticulation.

INTRODUCTION

Until Lazell (1969) described the new species *Phenacosaurus orcesi* from two localities in Ecuador, the anoline lizards separated as the genus *Phenacosaurus* had been known only from Colombia and from just over the border in Venezuela. A summary of new information has been reported in Williams *et al.* (1996).

Now still another small but distinctive new species, represented by a unique specimen, deposited in the collections of the Sociedad de Ciencias Naturales "La Salle," Caracas, most similar to the other tepui species, *P. neblininus,* from Cerro de La Neblina, provides the easternmost representative of the genus from Chimantá Tepui in Venezuela.

The new species is named after the late Carlos Todd, long active in conservation work (Gorzula, 1987), who participated in the exploration of Chimantá Tepui that resulted in the discovery of the new species *Phenacosaurus carlostoddi.*

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DESCRIPTION

Phenacosaurus carlostoddi, new species

Holotype. SCN 10351, adult female, coll. S. Gorzula and A. Farrera, February 1, 1984.

Type Locality. The southern high plateau of Abacapa-tepui (05°12′N, 62°19′W) (CHIMANTÁ V.), Estado Bolivar, Venezuela, 2,200 m.

Diagnosis. A small phenacosaur closest to *P. neblininus,* but differing from it and all other phenacosaurs in having the ear opening larger than the interparietal, rather than smaller or much smaller, in having the circumnasal in broad contact with the rostral not at all in contact with the first supralabial, instead of having a scale intervene between the circumnasal and the sulcus between the first supralabial and rostral, and an apparently generally darker coloration, and in having the belly with bold dark reticulation.

It (and *neblininus*) differs from the *orcesi* group, to which *neblininus* was first referred, in the condition of the fourth toe. Lamellae (scales wider than long, distally imbricate) in the fourth toe are restricted to phalanges ii and iii.

Description. Head: Casque indicated by distinct lateral and occipital ridges.

Dorsal head scales (Fig. 1): Antorbital area—Scales smooth or weakly rugose, small at the tip of the snout and posterior to the circumnasals and between the canthals and a median row of larger scales. Post rostrals 8, including the circumnasals and the anteriormost loreals of both sides. *The latter on both sides just exclude the circumnasals from the sulcus between the rostral and the first supralabial.* Dorsally 4 scales between the circumnasals.

Canthals 6 on the left side, 7 on the right, rounded or very bluntly keeled. On both sides the anteriormost canthal separated from the circumnasal by 2 scales, one behind the other. Six scales between the second canthals across the frontal depression.

Frontal depression shallow, the scales within it all larger than those at the tip of the snout.

Orbital area—Scales of the supraorbital semicircles large, smooth or lightly rugose, 2 pairs in contact. Scales of the supraocular area smooth or very weakly shagreened. On each side the 3 largest of

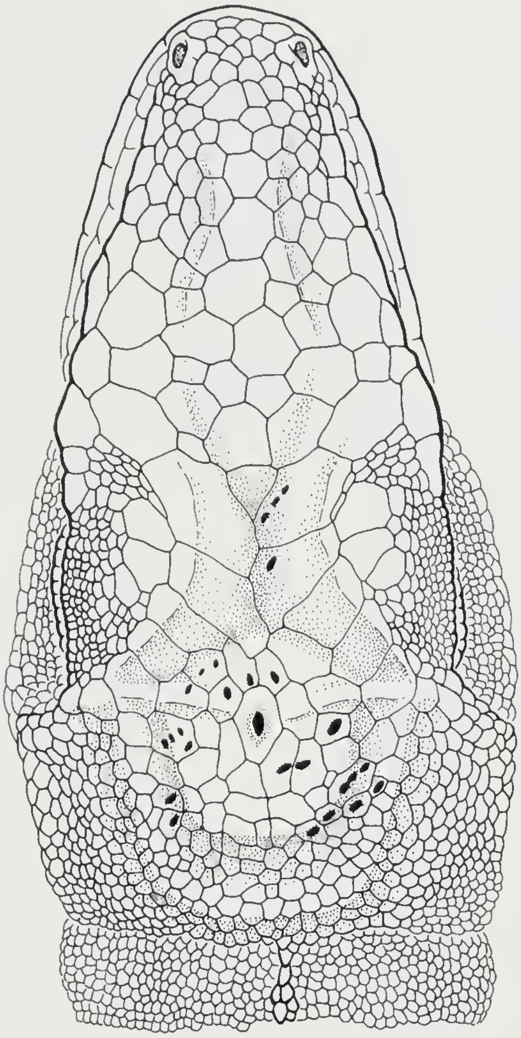


Figure 1. *Phenacosaurus carlostoddi,* holotype, SCN 10351: Dorsal view of head. The black areas on the parietal scales and on some scales of the semicircles represent the characteristic pustulations referred to in the text.

the supraocular scales forming a medial arc, the 2 largest of these in contact with the supraorbitals, the third separated by granules. Lateral scales of the supraocular region somewhat enlarged medially, but always sharply smaller than the medial supraoculars and becoming granular at the superciliary border. One (right side) or 2 (left side) anteriormost superciliaries short, bluntly keeled, quadrate or wedge-shaped, and followed only by granules not distinguishable from the adjacent granules of the supraocular region.

Parietal area—Scales on the boundary ridges of this area not significantly larger than adjacent nape or supratemporal scales.

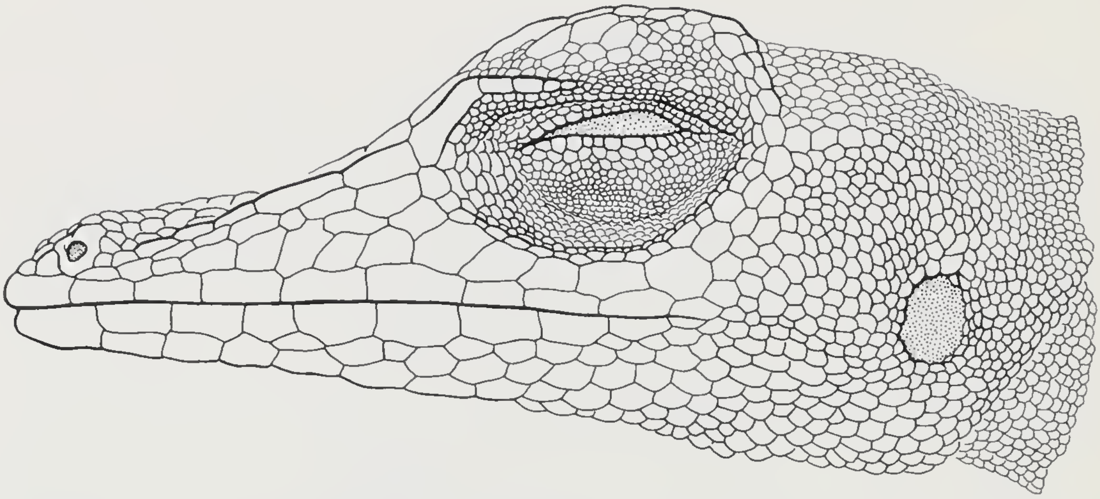


Figure 2. *Phenacosaurus carlostoddi,* holotype, SCN 10351: Lateral view of head.

No pustulations or rugosities on the scales of the lateral and occipital ridges. About 3 rows of scales lateral and posterior to the interparietal and 1–2 rows anterior to it distinctly enlarged. These enlarged parietal scales and the interparietal itself distinctly smaller than the larger scales of the frontal depression. An indistinct parietal eye. The interparietal scale diamond-shaped, small, *smaller than the rather large ear,* and separated by 1–2 scales from the semicircles. All scales surrounding the interparietal swollen, rugose with irregular raised areas and abundant pustulation, characteristic of other phenacosaur species also, overlying rugosities on the underlying bone. Some scale borders difficult to see. About 7 or 8 scales, decidedly irregular in shape and size between the interparietal and the subgranular nape scales.

Lateral head scales (Fig. 2): Loreal rows 3 on each side. Total number of loreals 17 on right side, 14 on left.

Preoculars 2 on each side, the uppermost in contact with the second canthal. Suboculars 4 on right side, 5 on left. Postoculars not well defined grading into the lower temporals. Seven to 8 supralabials to below the center of the eye.

Lower temporal scales slightly convex, smooth, juxtaposed, larger near the postoculars into which they grade. A weakly differentiated intertemporal zone of 1 row grading from the largest next to the postoculars to scales not distinguishable from nape scales.

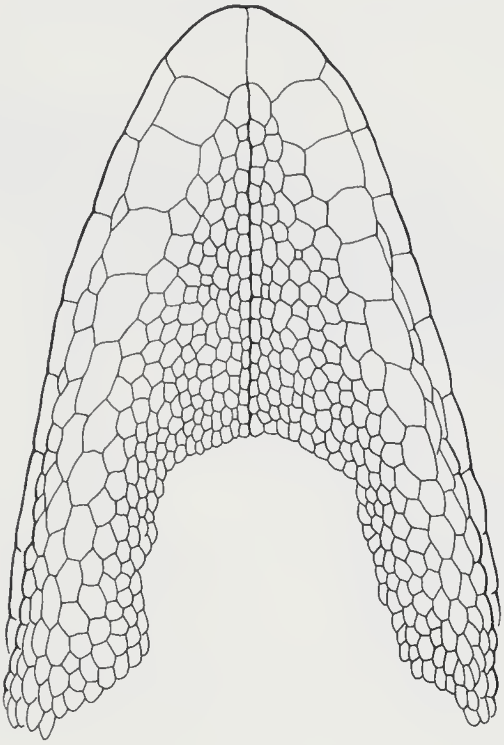


Figure 3. *Phenacosaurus carlostoddi,* holotype, SCN 10351: Ventral view of throat.

Upper temporals immediately above the intertemporal row small, flat, and smooth, subequal, abutting above on a zone demarcated by a slight ridge, surrounding the parietal area.

Ear opening on both sides, vertically ovoid, the narrower end above, its vertical dimension 6–8 times the height of the highest crest scales, relatively larger than the ears of any other species of the genus, larger than the interparietal.

Ventral head scales (Fig. 3): Mental almost completely divided, very bluntly indented, in contact with 4 postmentals between the infralabials, 1 first sublabial on each side, each about 4–5 times the size of the 2 medial gulars, which are themselves somewhat larger than the gulars posterior to them. Two additional sublabials on the right side, 3 on the left, in contact with the infralabials.

Central gulars small, smooth, swollen, juxtaposed, subrectangular, becoming somewhat larger and distinctly polygonal toward the sublabials.

Trunk (Figs. 5 and 6): An indistinct and at intervals interrupted crest of triangular scales, sometimes in 2 rows, sometimes in 1 row, always low, but of varying heights, and never much larger

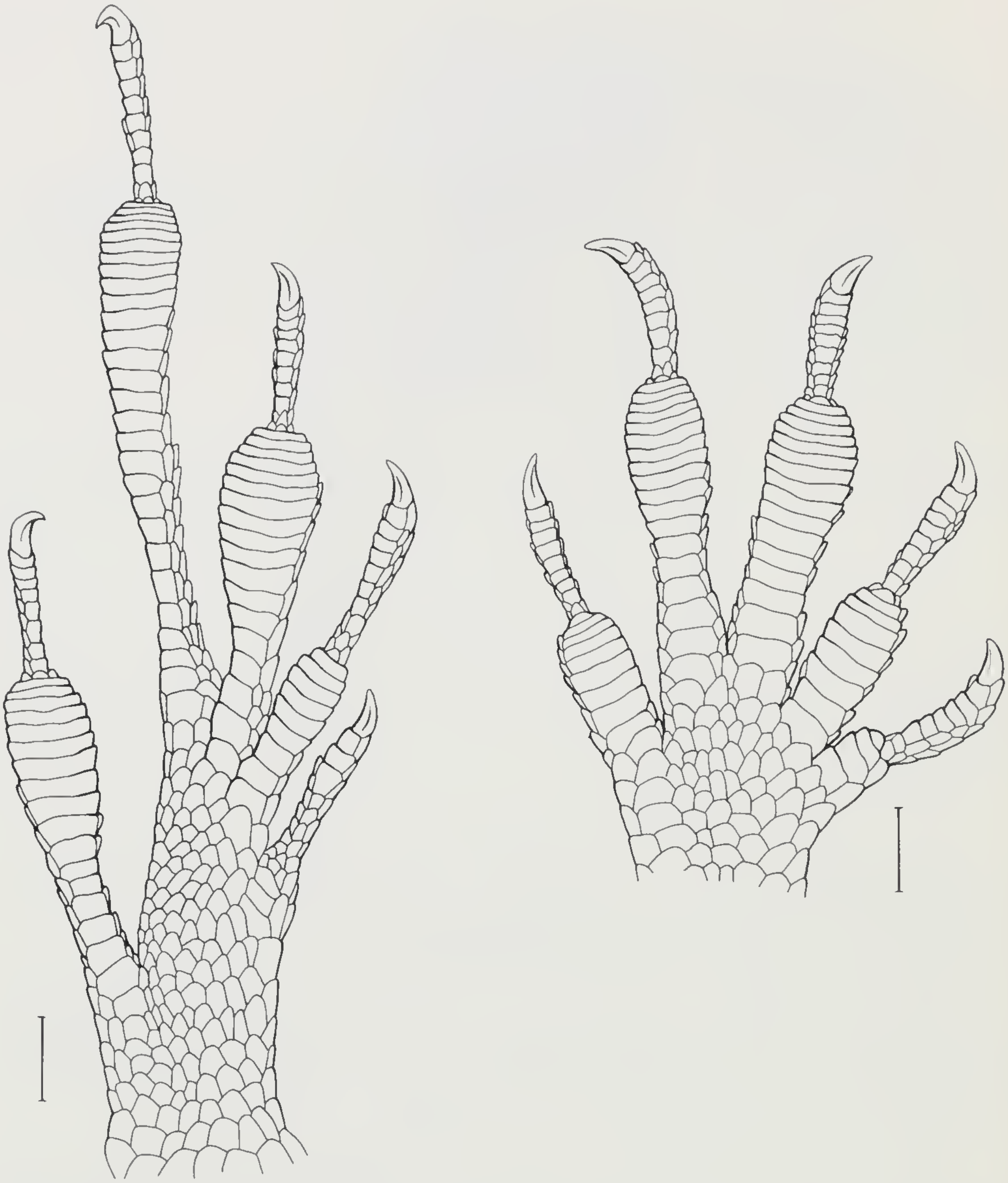


Figure 4. A subdigital view of the toes and hands of the holotype of *P. carlostoddi,* SCN 10351, to show that the fourth toe has the lamellar condition restricted to phalanges ii and iii. This feature has been confirmed in two paratypes of *P. neblininus,* USNM 322911 and 322912.

than the paravertebrals. Paravertebral and flank scales subequal, flat or slightly swollen, round, weakly rugose, tending to be in transverse rows, in contact paravertebrally, separated on lower flanks by naked skin or, in part, by granules, grading into ventrals. Ventrals smooth, oval, in transverse rows, subimbricate or separated by naked skin, larger than any dorsals.

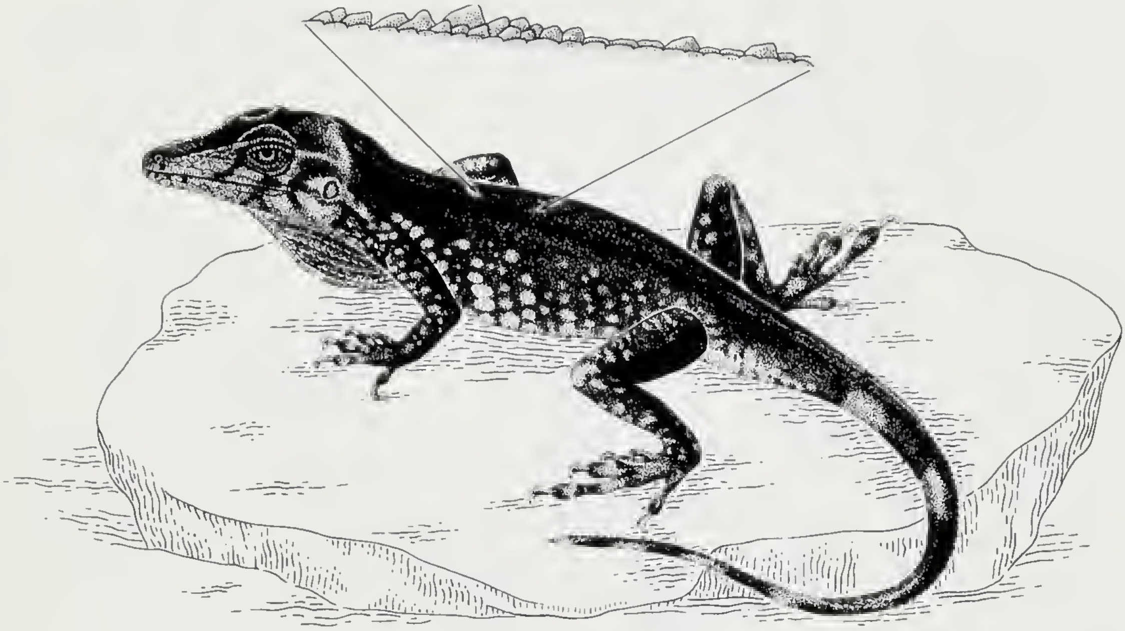
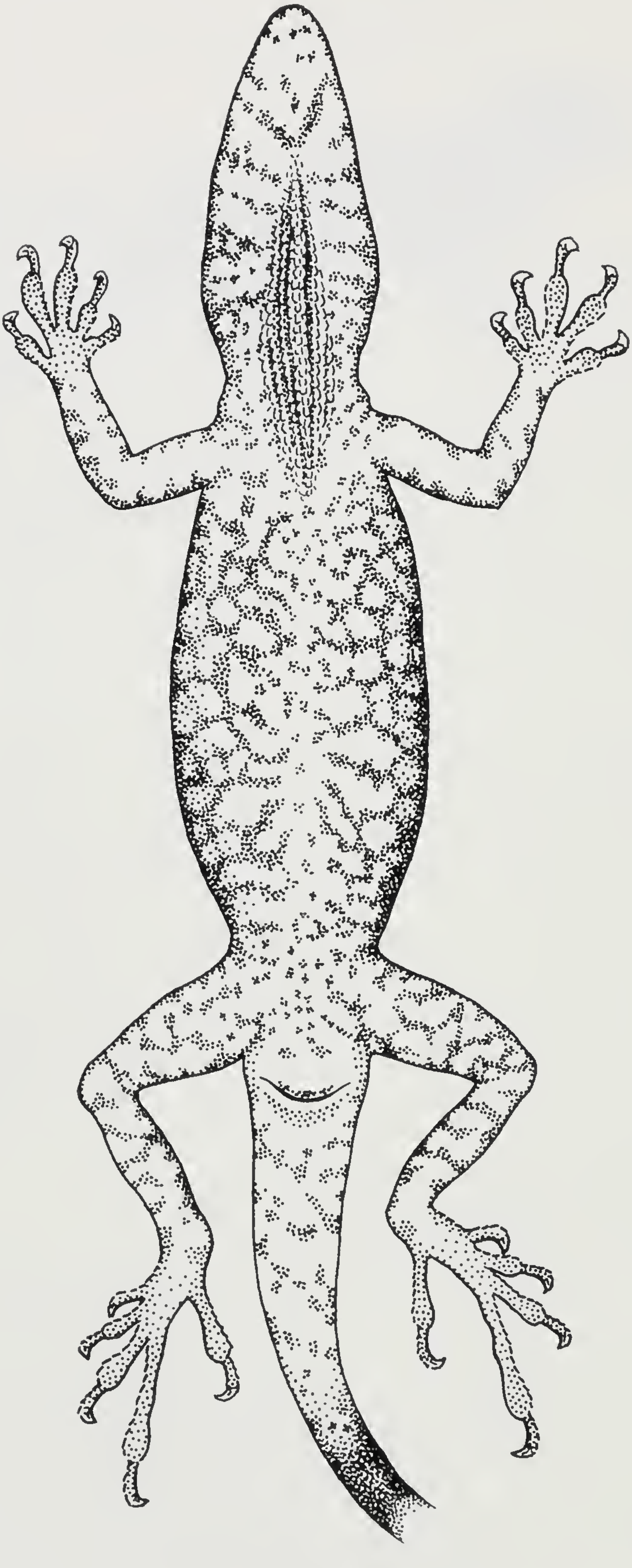


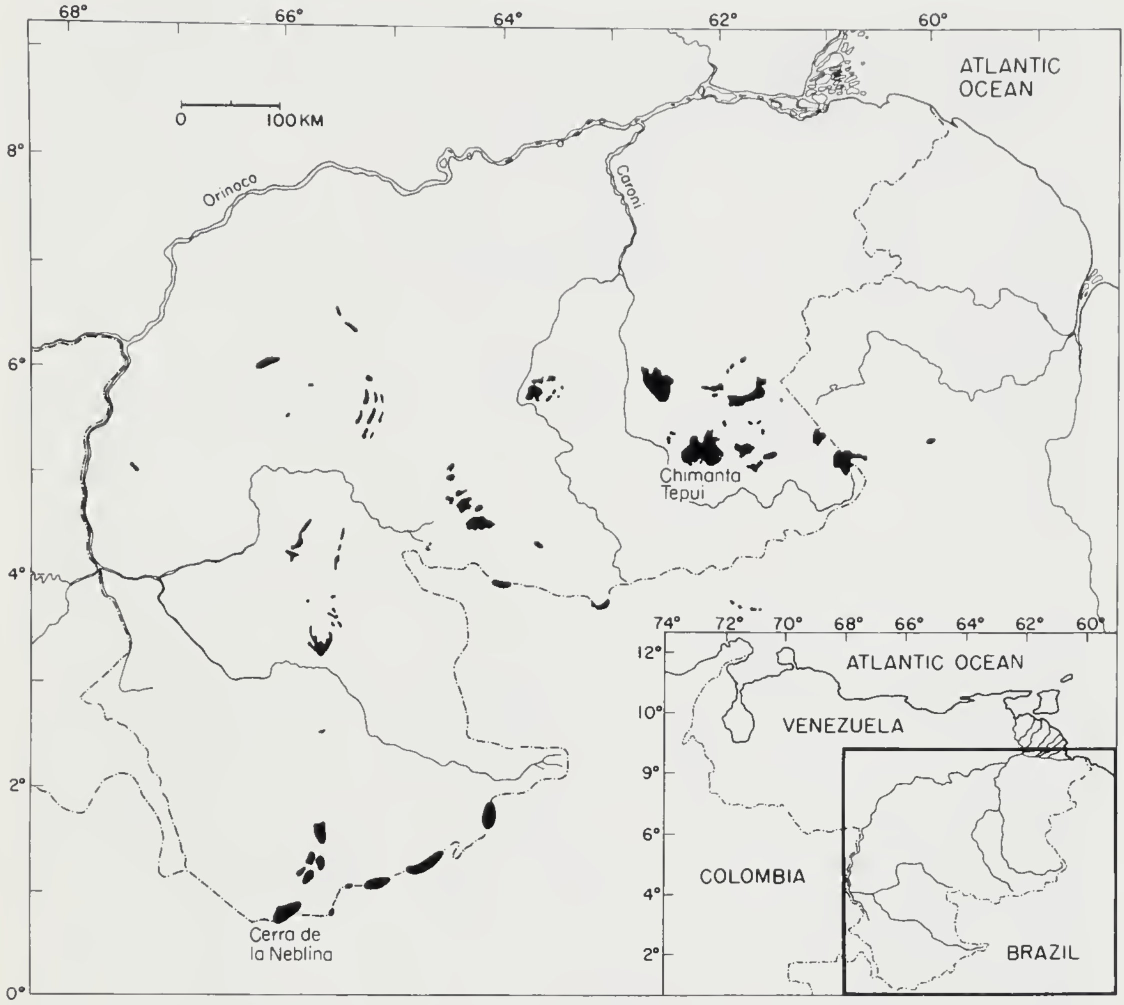
Figure 5. *Phenacosaurus carlostoddi,* holotype, SCN 10351: Lateral view of entire animal.

Limbs (Fig. 4): Upper arm scales smooth, larger and imbricate anteriorly and ventrally, smaller and juxtaposed or separated dorsally, posteriorly, and ventrally. Lower arm scales keeled, imbricate anteriorly and ventrally, smooth, juxtaposed or subimbricate dorsally, posteriorly and ventrally. Thigh scales anteriorly keeled, imbricate, posteriorly smooth subgranular. Supradigitals rugose rather than keeled. *The toe pad of the fourth toe restricted to the intermediate phalanges (ii and iii).* (Two or 3 scales are again wider than long at the insertion of the proximal phalanx of the fourth toe into the palm, but they are not believed to be lamellae. They are described as lamella-like.) All other toes are subdigitally totally lamellar. *Eighteen lamellae under phalanges ii and iii of fourth toe. All fingers subdigitally lamellar.*

Tail (Fig. 5): Distinctly compressed. A single median crest (except on the tail base where the relevant scales are low and small), becoming larger, sharply keeled and conspicuously dentate about 10 mm behind the hindlimbs. Lateral scales not keeled near base of tail, small, quadrate, rugose, becoming larger and distinctly keeled posteriorly. No enlarged postanals (female). Scales behind vent smooth, becoming keeled only 20–22 mm behind vent.

Dewlap (Figs. 5 and 6): Posteriorly just reaching beyond the level of the insertion of the forelimbs. Edge scales much smaller

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4°
2°
ATLANTIC OCEAN
VENEZUELA
COLOMBIA
BRAZIL

Figure 7. "Pantepui" *sensu* Mayr and Phelps (1967), showing the locations of Cerro de la Neblina and Chimantá Tepui.

than ventrals, oval. Lateral scales abruptly larger, but still smaller than ventrals, in rows, triangular or trapezoidal.

Size: Snout–vent length (SVL) 55 mm, tail 73 mm.

Color in Life (from Gorzula's Field Notes). "Distinct black markings on an off-white background on the head. Dorsum with light brown markings. Bluish gray color on the gular fan when extended."

Color as Preserved. Head and body black dorsally, with very vaguely indicated coarse lighter mottling. Suboculars and su-

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Figure 6. *Phenacosaurus carlostoddi,* holotype, SCN 10351: Ventral view of entire animal.

pralabials light with spotting below middle of eye and below second canthals. Loreals mostly light on right side, mostly dark on left side. Light spotting in front, above, and behind arms and in axilla. Limbs above black, vaguely spotted or mottled. Throat with small black spots and streaks. Belly and anterior tail boldly reticulate with black, the reticulations broken at midline. Limbs below light centrally with black spotting on anterior and posterior margins. Posterior two-thirds of tail black.

Habitat. Found at about 11:00 A.M. in a small crack in the sandstone, near the top of a deep crevasse on a very exposed rock escarpment. There were only some stunted *Bonnetia roraimae* scrub and patches of vegetation within a radius of about 100 m.

Comment. Phenacosaurus carlostoddi would appear to be genuinely rare. From 1983 to 1987, 22 localities were explored on the Chimantá Massif. Gorzula visited and collected the herpetofauna of 16 of these localities, and others made similar collections at five of the remaining six localities. Collecting parties usually stayed 3–5 days at each locality. Gorzula has also collected amphibians and reptiles on the adjacent Angasima and Adanta tepuys, on Aprada Tepui, on Ptari Tepui, at a dozen or so localities on the Auyan Tepui Massif, at localities on the "Los Testigos" chain of tepuys, at three localities on Ilu Tepui, on Yuruani Tepui, and at two localities on Cuquenan Tepui. Gorzula has also collected at dozens of localities at intermediate elevations in the Gran Sabana. He reported the following:

> There was usually no problem in collecting "tepui species" once their habitat was known. *Phenacosaurus carlostoddi* and *Atractus steyermarki* were exceptions to this general rule. The only other high elevation anole was *Anolis chrysolepis eewi*, a short-legged rock-dweller, that turned up on widely separated tepuys at elevations above 1,700 m.
>
> *Associated Species.* Also collected from "Chimantá V" were *Ololygon* sp. (an undescribed species common around swamps on most tepuys in the Gran Sabana region) [now *Scinax* sp. *fide* Duellman and Wiens, 1992], *Arthrosaura* sp. (an undescribed species collected at various localities but only on the Chimantá Massif) and *Stefania ginesi* (very common in swamps and in adjacent *Brocchinea hectioides*, apparently

endemic to the Chimantá Massif but with closely related species or subspecies on most other tepuys in the Gran Sabana region [Duellman and Hoogmoed, 1984].

DISCUSSION

Ernest E. Williams

It is especially necessary to begin to sort out the similarities and differences within *Phenacosaurus* with seven new taxa described since the last revision (Lazell, 1969), which recognized just three species.

Three groups are currently recognizable in the genus: the *heterodermus* group, the *orcesi* group, and the *neblininus* group:

I. The *heterodermus* group (two subgroups) is defined by scale heterogeneity: the round flat enlarged scales intermingled with smaller scales and granules. All the subdigital scales of the hands and feet are always totally lamellar (wider than long and with a distal free edge), as in the species *heterodermus*.

    (1) The *heterodermus* subgroup *sensu stricto* (strongly heterogeneous flank scalation, well-developed casquing, moderate to giant size) includes *heterodermus* Duméril and Duméril, 1851 (maximum SVL 76 mm), the Colombian giant *inderenae* Rueda and Hernández-Camacho, 1988 (maximum SVL 118 mm), and the Ecuadorian giant *vanzolinii* Williams, Orces, Matheus, and Bleiweiss, 1996 (maximum SVL 104 mm).

    (2) The *nicefori* subgroup (weakly heterogeneous flank scalation, casquing dependent on size, small or near giant) includes *nicefori* Dunn, 1944, a species now known to be smaller than *heterodermus* (maximum SVL 63 mm) and *tetarii* Barros, Williams, and Viloria, 1996, (maximum SVL 85 mm), a near-giant species tentatively referred to *nicefori* by Alemán (1953) and Lazell (1969) and now shown by an additional two specimens to be a valid species.

II. The *orcesi* group differs from the *heterodermus* group by the absence of heterogeneity in flank scales (the enlarged flat round scales). All subdigitals of the hands and feet are totally lamellar, as in the *heterodermus* group.

The *orcesi* group (homogeneous flank scalation, relatively poorly developed casquing, small size) includes Ecuadorian *orcesi* Lazell, 1969 (maximum SVL 59 mm), and Venezuelan (and probably Colombian: the Sierra de Perijá occurs on both sides of the border) *euskalerriari* Barros, Williams, and Viloria, 1996 (maximum SVL 53 mm) and a single juvenile from Peru (Williams and Mittermeier, 1991) (SVL 32 mm), which was left unnamed because of its juvenile status.

III. The *neblininus* group again differs from the *heterodermus* group in the absence of heterogeneity in its flank scalation but is defined by the fourth toe of the hindfoot having the most distal and the most proximal phalanx nonlamellar (the distal scales narrow = nonlamellar and two or three of the most proximal lamella-like). All the subdigitals of the hands and four of the five digits of the feet are lamellar.

The *neblininus* group (homogeneous flank scales, poorly developed casque, small in size) are confined thus far to two tepuys in south-central and eastern Venezuela: the *neblininus* Myers, Williams, and McDiarmid, 1993, from Cerro de la Neblina (maximum SVL 63 mm) and *carlostoddi* Williams, Praderio, and Gorzula, 1996 (this paper) (maximum SVL 55 mm).

All the species of *Phenacosaurus* are poorly known, some because of the difficulty of collection, as may well be true of the *neblininus* group (Myers *et al.,* 1993:12–14; S. Gorzula, see earlier under Habitat). For the *heterodermus* group, the difficulty may be quite different. Special difficulty in species discrimination results from the extraordinary variability of *P. heterodermus,* as currently recognized.

It is almost certain, however, that the present concept of *P. heterodermus* is an unresolved complex of sibling species. Old material, discolored to a muddy brown by formaldehyde that was too strong and, as well, from inexact localities, is nearly useless for discrimination of species. New material collected from precise localities and preserved in a fashion that does not obscure color and pattern will be necessary to solve this problem. Above all, it will also be necessary to find new characters.

The fourth toe of the *neblininus* group is anomalous among the phenacosaurs. All the other phenacosaurs have all subdigitals lamellar. The *neblininus* group overlaps the variation ascribed to *Anolis* totally. In the fourth toe of the *neblininus* group phenacosaurs only the most restricted anoline toe pad—the subdigitals under phalanges ii and iii—is lamellar (wider than long, imbricate distally), as in some *Anolis.* In many other *Anolis,* some fraction of the subdigitals of the proximal phalanx is lamellar. Peterson (1983:270) cited *Anolis aequatorialis* as having half to two-thirds of the anterior portion of the proximal phalanx lamellar. *Phenacosaurus* was cited as possibly "unique" in having lamellae on all the subdigitals of the proximal phalanx of the fourth toe.

The discovery that the fourth toe of the *neblininus* group was anomalous for *Phenacosaurus* was very late, much too late for the fact to be recorded in Myers *et al.* (1993), indeed, well after the manuscript for this description of *carlostoddi* was "completed." In fact, in only two of the paratypes of *neblininus* has this "anomaly" been verified. Peterson (1983) was writing 10 years before the description of *neblininus,* before any but three species were considered valid. Peterson saw only *heterodermus,* but of the nine species now current only the two show the fourth toe of the hindfoot as anything but totally lamellar.

The paraphyly of *Anolis* relative to *Phenacosaurus* was suggested by Etheridge and de Queiroz (1988:312). Presumably the assumption of paraphyly would make *carlostoddi* and *neblininus* the most primitive known phenacosaurs, but this is not unequivocal. The *neblininus* group still shows the presumed synapomorphy of all the subdigitals of the hand and four of five of the feet (Fig. 4) being lamellar. Possibly the "anomaly" could be a homoplasious loss of the lamellar condition for the proximal phalanx of the fourth toe in only the *neblininus* group of phenacosaurs. Perhaps a totally lamellar condition of all the fingers and toes was the original condition of all the anolines.

Perhaps the reverse of the Etheridge and de Queiroz supposition is true. *Phenacosaurus* is not derived from within *Anolis.* Instead of the Venezuelan tepui species being most primitive, and the Colombian species being most derived, with *P. orcesi* and related forms being intermediate, the evolutionary scene might be very different. Instead, the totally lamellar condition of the subdigitals of the hands and the feet may be primitive for anoline lizards, the heterogeneous flank scalation primitive for the genus *Phe-*

nacosaurus, and a well-developed casque primitively restricted to large phenacosaurs.

Intriguing as this discussion might be, it would obviously be inappropriate to append this extensive and still incomplete work to a species description.

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DEEP-SEA PELAGIC FISHES FROM THE AZORES (EASTERN NORTH ATLANTIC) DEPOSITED IN THE MUSEUM OF COMPARATIVE ZOOLOGY

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JAMES E. CRADDOCK,[2,3] AND RICARDO S. SANTOS[1]

ABSTRACT. The meso- and bathypelagic fishes collected by the Woods Hole Oceanographic Institution from the Azores Economic Exclusive Zone and stored at the Museum of Comparative Zoology are reviewed and show a total of 9,260 specimens from 120 collections composing 153 species in 56 families. Twenty-eight species in 12 families are new to the area and are documented here in detail. A full list of all species and localities is included.

INTRODUCTION

The mesopelagic and bathypelagic fishes account for more than 35% of the total number of species reported from the Azores (Santos *et al.*, 1997). These two groups are diverse in the area, and various species can be found in the open ocean as well as in the narrow regions around the islands.

Interest in understanding the oceanography of the Azores resulted in a number of research programs in the region over the past 150 years. However, it was only with the expeditions of *Travailleur* and *Talisman* (Vaillant, 1888) that detailed reports on

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deep-sea fishes began. Late in the last century and during the first decades of this century, the scientific cruises of Prince Albert I of Monaco produced the beginnings of an inventory of the oceanic ichthyofauna of the Azores (e.g., Collett, 1896, 1905; Richard, 1905; Zugmayer, 1911, 1933; Roule, 1919; Roule and Angel, 1924). Other important meso- and bathypelagic material from the Azores was collected by the *Michael Sars* North Atlantic Deep Sea Expedition (e.g., Murray and Hjort, 1912; Koefoed, 1956, 1958; Bolin, 1959) and by several Danish expeditions with *Dana* (e.g., Jespersen, 1915; Regan and Trewavas, 1929; Ege, 1930, 1953; Nafpaktitis, 1968; Bertelsen *et al.,* 1976). Since then, several other countries have been involved in oceanic research programs in the Azorean region (e.g., France, Germany, Portugal, Russia, Sweden, and the United States).

In particular, several oceanographic expeditions to the Azores region were conducted by the Woods Hole Oceanographic Institution (WHOI) between 1928 and 1984. These cruises were aimed at investigations of the pelagic domain and the material collected is now archived at the Museum of Comparative Zoology (MCZ), Harvard University. Most of the specimens were fully identified at WHOI during ecological and biogeographical studies, but only selected parts of the collection have been used in publications (e.g., Borodin, 1931; Haedrich, 1964; Nafpaktitis *et al.,* 1977). Arruda (1997) produced a checklist of Azorean fishes primarily based on literature references. Many of his records are confirmed by the specimens cited in this paper.

We had the opportunity to study the eastern Atlantic collection housed in the MCZ, and based on those studies, we record the first documented occurrence of some meso- and bathypelagic fishes in the Azores region. In addition, we present a complete list of the fishes collected in the Azores by the WHOI expeditions.

MATERIAL AND METHODS

Following Santos *et al.* (1997) we consider Azorean waters as the Azores Economic Exclusive Zone (EEZ, Fig. 1). A complete listing of all the collecting stations and associated data of the 10 WHOI cruises done in the EEZ are shown in Appendix 1. These stations are also plotted in Figure 1. The station data are arranged

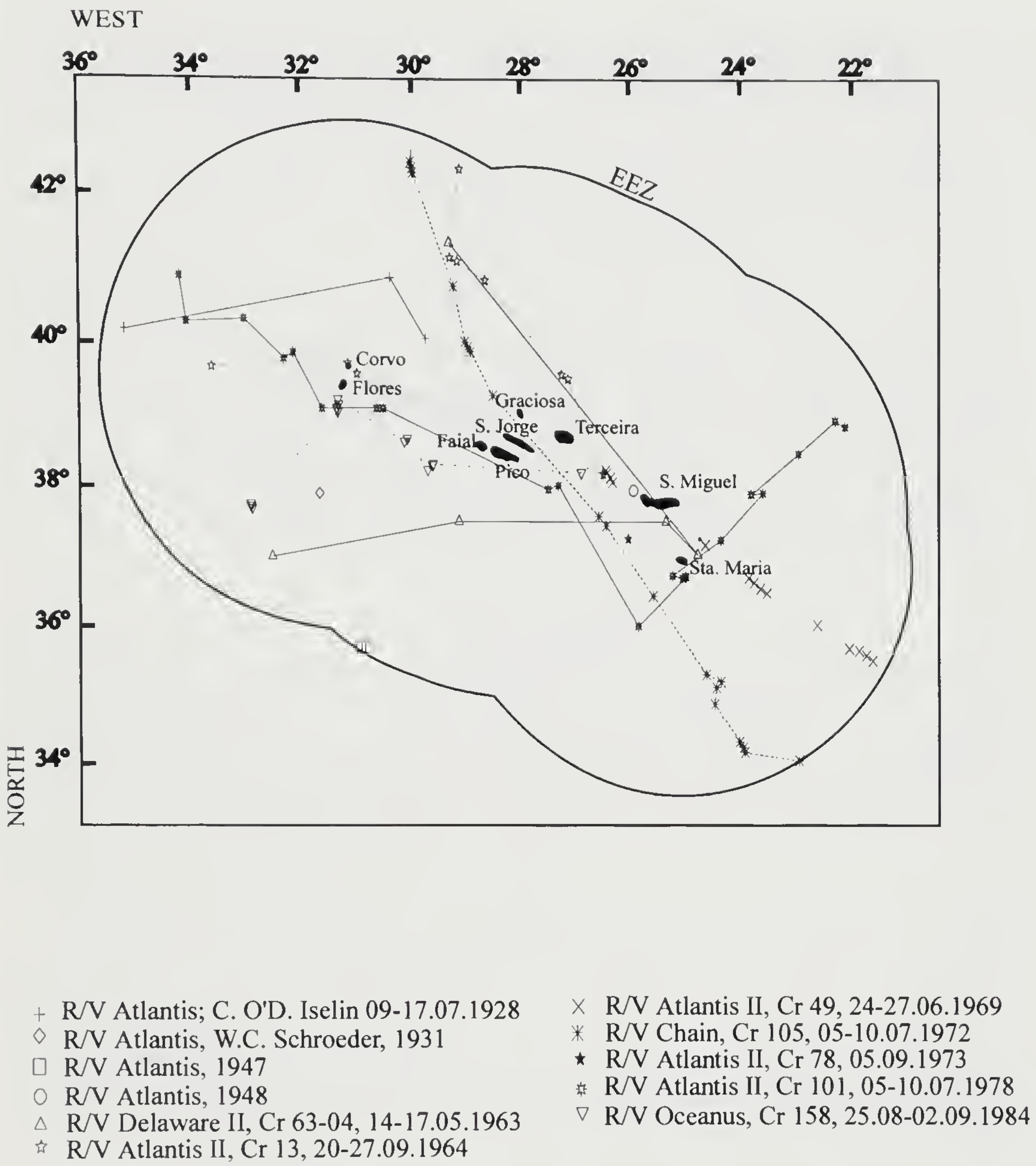
WEST
36°
34°
32°
30°
28°
26°
24°
22°
42°
40°
38°
36°
34°
NORTH
EEZ
Corvo
Flores
Graciosa
S. Jorge
Terceira
Faial
Pico
S. Miguel
Sta. Maria
+ R/V Atlantis; C. O'D. Iselin 09-17.07.1928
◇ R/V Atlantis, W.C. Schroeder, 1931
□ R/V Atlantis, 1947
○ R/V Atlantis, 1948
△ R/V Delaware II, Cr 63-04, 14-17.05.1963
☆ R/V Atlantis II, Cr 13, 20-27.09.1964
× R/V Atlantis II, Cr 49, 24-27.06.1969
⁎ R/V Chain, Cr 105, 05-10.07.1972
★ R/V Atlantis II, Cr 78, 05.09.1973
✲ R/V Atlantis II, Cr 101, 05-10.07.1978
▽ R/V Oceanus, Cr 158, 25.08-02.09.1984

Figure 1.

chronologically by cruise and referenced by field numbers. The field numbers refer to the collectors as follows: CODI refers to collections made by C. O'D. Iselin, RHB to collections made by Richard H. Backus and James E. Craddock, SUN to surface collections that accompanied the RHB stations, CEL to collections made by Charles E. Lea, and KEH to collections made by Karsten E. Hartel. The identification and distribution of the species found in the WHOI collections were reviewed and compared with Santos *et al.* (1997), Whitehead *et al.* (1984–1986), Hureau and Monod (1973), Quéro *et al.* (1990a), and numerous primary works. In addition, we compared the specimens with related material in the MCZ collections.

All records of species new to the area are outlined in the following section. Appendix 2 lists all of the remaining species found in the WHOI collections from the Azorean EEZ. Some rare species caught just outside the EEZ are also reported. Full data on MCZ collections are available at http://www.mcz.harvard.edu/fish. We follow the family nomenclature and arrangement of Nelson (1994). Fishes that could only be identified to genus or family are usually not included in Appendix 2 except in cases of rarity or of special interest.

RESULTS

The WHOI/MCZ collections from the Azores were taken at 120 stations fished from the surface to about 1,000 meters, usually with an open net (Appendix 1, Fig. 1). A computer search of the database at MCZ (MUSE) from the EEZ produced 1,198 lots and more than 9,260 specimens with 153 species in 56 families. The majority were mesopelagic (ca. 88%), followed by epipelagic (ca. 9%), and a small number of bathypelagic species.

Myctophidae is the largest family represented with 41 species from 646 collections and 70% of the specimens. Other families, such as the Stomiidae, Sternopthychidae, Gonostomatidae, Photichthyidae and Paralepididae, are reasonably well represented, both in terms of their specific diversity and total numbers (see Appendix 2).

Benthosema glaciale is the most numerous fish in any individual collection because it was abundant at two stations (RHB 2535, RHB 2536) made in the northern area of the EEZ. However, *Gonichthys coccoi, Lobianchia dofleini,* and *Lampanyctus pusillus* are the most commonly caught fish in the collections (Appendix 2). Of the 20 most abundant species, 65% belong to the Myctophidae. However, fishes in other families (e.g., *Argyropelecus hemigymnus, Vinciguerria attenuata,* or *Stomias boa*) are also common. Larvae represent fewer than 20% of the total number of fishes.

The collections add 28 species in 12 families to the Azores ichthyofauna (see below). Bathylagidae and Anotopteridae are new families to the area.

NEW RECORDS OF FISH SPECIES FOR THE AZORES

Bathylagidae

Bathylagus bericoides (Borodin, 1929)

Comments. Occurs in tropical, subtropical, and temperate waters of all oceans. Although reported from the northeast Atlantic (Cohen, 1984a), the MCZ material represents the first documented records from the Azores.

Azores Material. **61912,** R/V *Atlantis II* 49, RHB1917, 35°34′N 21°54′W, 135–140 m, 0045–0219 h, 25.VI.1969, 1:48 mm SL; **61909,** R/V *Atlantis II* 13, RHB1039, 40°47′N 28°41′W, 450–500 m, 2030–2350 h, 20.IX.1964, 2:29–116 mm SL; **61913,** R/V *Atlantis II* 49, RHB1928, 38°05′N 26°N29′W, 192–202 m, 0231–0408 h, 27.VI.1969, 1:105 mmSL; **149499,** R/V *Atlantis II* 101, CEL7833, 36°37′N 25°04′W, 50–170–80 m, 2146–2345 h, 09.VII.1978, 1:91 mm SL.

Bathylagus greyae Cohen, 1958

Comments. This species is generally tropical (Cohen, 1984a), but we have found numerous records from the Azores and adjacent waters.

Azores Material. **66131,** R/V *Atlantis II* 49, RHB1922, 36°32′N 23°49′W, 135–140 m, 0046–0221 h, 26.VI.1969, 1:90 mm SL; **149498,** R/V *Atlantis II* 101, CEL7837, 37°48′N 23°39′W, 350 m, 2211–0045 h, 10–11.VII.78, 1:67 mm SL; **150907,** R/V *Chain* 105, RHB2537, 42°17′N 29°59′W, 225–255 m, 0017–0135 h, 05.VII.1972, 1:33 mm SL; **150908,** R/V *Chain* 105, RHB2540, 39°55′N 29°03′W, 60–70 m, 2135–2250 h, 05.VII.1972, 2:62 mm SL; **150909,** R/V *Chain* 105, RHB2550, 35°03′N 24°30′W, 290–310 m, 0112–0235 h, 08.VII.1972, 1:45 mm SL.

Bathylagus longirostris Maul, 1948

Comments. Known from tropical and subtropical waters of the Atlantic, Pacific, and Indian oceans (Cohen, 1984a). Originally described from Madeira. Although these are the first two records from the Azores, the species is common just south of the area based on MCZ material.

Azores Material. **66184,** R/V *Chain* 105, RHB2552, 34°17′N 24°05′W, 60–70 m, 2158–2305 h, 08.VII.1972, ?; **91356,** R/V *Chain* 105, RHB2553, 34°12′N 24°01′W, 125–135 m, 2355–0105 h, 08–09.VII.1972, 2:90–125 mm SL.

Opisthoproctidae

Dolichopteryx spp.

Comments. Two forms of this genus, based on distinctive postlarvae, are included here. One of these is probably *D. longipes* which has been reported from Madeira (Cohen, 1984b).

Azores Material. **66370,** R/V *Chain* 105, RHB2543, 39°10′N 28°33′W, 250–260 m, 0540–0815 h, 06.VII.1972, 1:27 mm SL; **66348,** R/V *Oceanus* 158, KEH8477, 37°35′N 32°55′W, 600 mwo, 0204–0325 h, 30.VIII.1984, 1:29 mm SL; **66345,** R/V *Atlantis II* 13, RHB1041, 39°24′N 27°11′W, 220–300 m, 1405–1830 h, 21.IX.1964, 1:22 mm SL.

Rhynchohyalus natalensis (Gilchrist and von Bonde, 1924)

Comments. This species was caught on the western edge of the EEZ and is included here because of the broad range suggested by other MCZ specimens from the Canaries (MCZ96900, MCZ66428) and from the western North Atlantic as far north as 39°28′N (MCZ60718). The only other northeast Atlantic record is from the stomach of a tuna fish at Madeira (Maul, 1946; Cohen, 1984c).

Material. **66429,** R/V *Atlantis II* 13, RHB1046, 39°30′N 35°58′W, 425–500 m, 0915–1237 h, 27.IX.1964, 1:37 mm SL.

Alepocephalidae

Bellocia koefoedi (Parr 1951)

Comments. This endemic North Atlantic bathypelagic species lives between 2,500 and 5,850 m (Markle and Quero, 1984; Markle and Sazonov, 1990). An MCZ specimen was caught at the southwest corner of the EEZ close to the type locality. There are few records of this species for the northeastern Atlantic.

Azores Material. **36636,** R/V *Atlantis II,* ATLAN4715, 35°37′N 30°57′W, 3,200 mwo, 1312–? h, 16.VII.1947, 1:135 mm SL.

Platytroctidae

Sagamichthys schnakenbecki (Krefft 1953)

Comments. A 24-mm SL postlarva found in the MCZ material from the middle of the EEZ confirms Quéro *et al.* (1984) mapping. This species was not indicated for the Azores in Matsui and Rosenblatt (1984). The eastern Atlantic MCZ material includes more than 20 records of postlarvae and juveniles from 16°N to 56°N, with some just to the east of the Azores. MCZ material also includes several records from off the east coast of North America that have not been reported previously (e.g., MCZ75508).

Azores Material. **128329,** R/V *Chain* 105, RHB2538, 40°42′N 29°15′W, 560–600 m, 0950–1225 h, 05.VII.1972, 1:27 mm SL.

Gonostomatidae

Cyclothone livida Brauer 1902

Comments. Recorded from southern Iceland to Angola (Badcock, 1984a; Quéro *et al.,* 1990b). One MCZ collection documents its occurrence in the Azores. Additional MCZ material shows that *C. livida,* formerly thought to be an eastern Atlantic endemic (Miya and Nishida, 1996), actually ranges across the Atlantic to 55°W between 3°N and 12°N.

Azores Material. **143321,** R/V *Atlantis II* 49, RHB1924, 37°04′N 24°42′W, 750–830 m, 0808–1005 h, 26.VI.1969, 1:34 mm SL.

Cyclothone pseudopallida Mukhacheva 1964

Comments. A wide-ranging species in all tropical, subtropical, and temperate oceans. *C. pseudopallida* was expected to be in the Azores, but these are the first confirmed records. In the Canaries, this species is a nonmigrant and is restricted to depths between 550 and 800 m (Badcock, 1970).

Azores Material. **142489,** R/V *Atlantis II* 13, RHB1036, 42°20′N 29°09′W, 470–520 m, 1600–1830 h, 19.IX.1964, 1:34 mm SL; **142501,** R/V *Atlantis II* 49, RHB1919, 35°56′N 22°40′W, 650–750 m, 0708–1030 h, 25.VI.1969, 3:34–37 mm SL; **142502,** R/V *Atlantis II* 49, RHB1924, 37°04′N 24°42′W, 750–830 m, 0808–1005 h, 26.VI.1969, 3:34–37 mm SL.

Sternoptychidae

Argyropelecus gigas Norman 1930

Comments. A widespread species in all oceans. Badcock (1984b) infers that the species should occur in the Azores. However, based on the MCZ material, it is rare in the area, with one specimen, but it is progressively more common to the south and east.

Azores Material. **137182,** R/V *Atlantis II* 49, RHB1919, 35°56′N 22°40′W, 650–750 m, 0708–1030 h, 25.VI.1969, 1:16 mm SL.

Polyipnus polli Schultz 1961

Comments. The species is included based on a single specimen caught at the northwest edge of the Azores, which is the northernmost record. This eastern Atlantic endemic is also known from the Grand Meteor Bank (Badcock, 1984b), the Canaries (MCZ135280), and further south (Quéro *et al.,* 1990c; Harold, 1994).

Material. **149500,** R/V *Atlantis II* 101, CEL7816, 42°05′N 35°35′W, 1,000 m, 2355–0240 h, 03–04.VII.78, 1:25 mm SL.

Stomiidae

Aristostomias grimaldii Zugmayer 1913

Comments. This species is reported for the Atlantic, Pacific, and Indian oceans but is rarely caught in the eastern North Atlantic. According to Goodyear (1990) this is the second record of *A. grimaldii* for that area. The MCZ material shows a concentration of this species along the east coast of North America, between 40°N and 25°N.

Azores Material. **150372,** R/V *Atlantis II* 101, CEL7833, 36°37′N 25°04′W, 350–170–80 m, 2146–2345 h, 09.VII.1978, 1: 85 mm SL.

Astronesthes gemmifer Goode and Bean 1896

Comments. An Atlantic, Pacific, and Indian Ocean species that occurs south of 45°N. Gibbs (1984a) maps the possible occurrence in the Azores area; however, the MCZ material probably represents the first documented records.

Azores Material. **133383,** R/V *Atlantis II* 49, RHB1919, 35°56′N 22°40′W, 650–750 m, 0708–1030 h, 25.VI.1969, 1:25 mm SL; **133387,** R/V *Chain* 105, RHB2555, 34°00′N 22°55′W, 470–520 m, 1002–1215 h, 09.VII.1972, 1:20 mm SL.

Astronesthes micropogon Goodyear and Gibbs 1970

Comments. A member of the "cyaneus" group as defined by Goodyear and Gibbs (1970), who noted that 35°N is the northern limit of its range. We know only one record from the Azores. The specimen is the northernmost record from the eastern Atlantic.

Azores Material. **91742,** R/V *Atlantis II* 49, RHB1918, 35°36′N 22°05′W, 169–175 m, 0231–0409 h, 25.VI.1969, 1:73 mm SL.

Astronesthes neopogon Regan and Trewavas 1929

Comments. A. neopogon is restricted to the North Atlantic and was described from just outside the Azorean EEZ. The MCZ specimen seems to be only the third northeastern Atlantic record since Maul (1956) described specimens from Madeira.

Azores Material. **149502,** R/V *Atlantis II* 101, CEL7832, 36°N 25°W, 350–190 m, 0050–0345 h, 09.VII.1978, 1:81 mm SL.

Eustomias macrurus Regan and Trewavas 1930

Comments. The species is known from the Atlantic, Pacific, and Indian oceans. This is the first record for the eastern Atlantic north of 6°N. It probably indicates that *E. macrurus* is more widely distributed in the eastern Atlantic than previously thought (Gibbs and Barnett, 1990). It is widespread in the western North Atlantic from 30°S to about 42°N (Gibbs and Barnett, 1990).

Azores Material. **149504,** R/V *Atlantis II* 101, CEL7838, 37°47′N 23°52′W, 350 m, 0045–0347 h, 11.VII.1978, 1:70 mm SL.

Melanostomias valdiviae Brauer 1902

Comments. The species is known from all oceans. In the eastern Atlantic it occurs to about 35°N (Gibbs, 1984b), but this is the first confirmed record from the Azores. Additional specimens of the species might be expected in the southern part of the area based on its known distribution.

Azores Material. **132155,** R/V *Atlantis II* 49, RHB1918, 35°36′N 22°05′W, 169–175 m, 0231–0409 h, 25.VI.1969, 1:143 mm SL.

Stomias brevibarbatus Ege 1918

Comments. A widespread North Atlantic species that Gibbs (1984c) did not report from the Azores. MCZ material and Coad (1986) record it as far north as Canadian waters in the western Atlantic. MCZ records show the species occurring in the Azores, with other records to the west and southeast of the area. This species was recently reported in the Gulf of Mexico (Sutton and Hopkins, 1996).

Azores Material. **128677,** R/V *Atlantis II* 49, RHB1928, 38°05′N 26°29′W, 192–202 m, 0231–0408 h, 27.VI.1969, 1:129 mm SL.

Trigonolampa miriceps Regan and Trewavas 1930

Comments. This rarely caught species is usually thought to be antitropical in the Atlantic Ocean, but we have seen an MCZ specimen from just off the Gulf of Guinea at 0°30′S. Gibbs and Barnett (1990) and Gibbs (1984b) note the species far north of and far south of the Azores. The MCZ material adds the first records for the Azores based on three specimens, all from the northern portion of the area.

EEZ Material. **114690,** R/V *Atlantis II* 13, RHB1039, 40°47′N

28°41′W, 450–500 m, 2030–2350 h, 20.IX.1964, 1:50 mm SL; **62186,** R/V *Chain* 105, RHB2542, 39°47′N 28°57′W, 165–175 m, 0102–0222 h, 06.VII.1972, 1:30 mm SL; **149503,** R/V *Atlantis II* 101, CEL7818, 40°50′N 34°11′W, 1,000 m, 2120–0040 h, 04–05.VII.1978, 1:45 mm SL.

Paralepididae

Uncisudis quadrimaculata (Post 1969)

Comments. The species is endemic to the eastern central Atlantic (Post, 1990). The MCZ material contains four lots of larvae from 39°N. Two of these are from within the EEZ and two from just to the west. The samples were caught near the surface at dusk or at night.

Azores Material. **68562,** R/V *Atlantis II* 13, RHB1043, 39°28′N 31°00′W, 20–35 m, 1920–2332 h, 23.IX.1964, 5:18–24 mm SL; **68563,** R/V *Atlantis II* 13, RHB1045, 39°34′N 33°37′W, 15–32 m, 1930–2325 h, 26.IX.1964, 2:33–38 mm SL.

Anotopteridae

Anotopterus pharao Zugmayer 1911

Comments. This species is antitropical in the Atlantic and Pacific oceans (Maul, 1973a; Post, 1984). Adults are rare in collections, probably due to gear selectivity (Heemstra, 1990). We include the species based on two postlarvae from the Azores. We have seen an additional postlarva (MCZ73016) from just outside the EEZ and one 265-mm SL juvenile (MCZ43141) found in the stomach of an *Alepisaurus brevirostris* at 40°17′N 36°07′W (Haedrich, 1964).

Azores Material. **73018,** R/V *Atlantis II* 49, RHB1924, 37°04′N 24°42′W, 750–830 m, 0808–1005 h, 26.VI.1969, 1:15 mm SL; **73020,** R/V *Chain* 105, RHB2549, 35°08′N 24°25′W, 40–50 m, 2340–0102 h, 07.VII.1972, 1:22 mm SL.

Myctophidae

Hygophum reinhardtii (Lütken 1892)

Comments. A widely distributed, bipolar species found across the subtropical and tropical Atlantic Ocean to about 40°N (Nafpaktitis *et al.,* 1977). The MCZ material contains the first confirmed records and shows that the southern Azores region is the northern edge of the range of this species in the eastern Atlantic. *H. reinhardtii* appear to be quite common south of 38°N within the Azores, and based on Nafpaktitis *et al.* (1977) the species would be expected to occur there. All the specimens were caught near the surface at night by neuston net.

Azores Material. **114801,** R/V *Atlantis II* 49, SUN1918, 35°36′N 22°05′W, surface, 0000–0330 h, 25.VI.1969, 2:35–45 mm SL; **114802,** R/V *Atlantis II* 49, SUN1920, 36°23′N 23°35′W, surface, 0000–0400 h, 25.VI.1969, 8:15–39 mm SL; **114803,** R/V *Atlantis II* 49, SUN1920, 36°23′N 23°35′W, surface, 0000–0400 h, 25.VI.1969, 2:27–30 mm SL; **114804,** R/V *Atlantis II* 49, SUN1921, 36°27′N 23°42′W, surface, 0000–0415 h, 25.VI.1969, 3:24–31 mm SL; **114805,** R/V *Atlantis II* 49, SUN1921, 36°27′N 23°42′W, surface, 0000–0415 h, 25.VI.1969, 4:20–29 mm SL; **114810,** R/V *Chain* 105, SUN2545, 37°23′N 26°33′W, surface, 0000–0215 h, 07.VII.1972, 1:30 mm SL; **114811,** R/V *Chain* 105, SUN2546, 37°20′N 26°30′W, surface, 0000–0345 h, 07.VII.1972, 4:30–38 mm SL; **114908,** R/V *Atlantis II* 49, RHB1920, 36°23′N 23°35′W, 63–65 m, 2045–2218 h, 25.VI.1969, 2:37–40 mm SL; **114993,** R/V *Chain* 105, RHB2552, 34°17′N 24°05′W, 60–70 m, 2158–2305 h, 08.VII.1972, 1:13 mm SL.

Lampadena anomala Parr 1928

Comments. L. anomala occurs in subtropical and tropical waters of the Atlantic, Pacific, and Indian oceans (Nafpaktitis *et al.,* 1977; Bekker, 1983). It is uncommon throughout all of its range. Swinney (1991) reports the occurrence of the species south of Madeira. We here confirm one specimen from the Azores and note others from southeast of the area (MCZ 96916).

Azores Material. **149506,** R/V *Oceanus* 158, KEH8489, 38°06′N 29°44′W, 400 mwo, 0010–0103 h, 02.IX.1984, 1:62 mm SL.

Lampanyctus cuprarius Taning 1928

Comments. A bipolar subtropical species (Nafpaktitis *et al.,* 1977) that is found principally south of 42°N on both sides of the Azores EEZ. MCZ material confirms this species for the Azores.

Azores Material. **112931,** R/V *Chain* 105, RHB2553, 34°12′N 24°01′W, 125–135 m, 2355–0105 h, 08.VII.1972, 2:46–65 mm SL; **151346,** R/V *Atlantis II* 101, CEL7838, 37°47′N 23°52′W, 350 m, 0045–0347 h, 11.VII.1978, 4:45–57 mm SL.

Lepidophanes gaussi (Brauer 1906)

Comments. A bipolar subtropical species that is found principally south of 37°N that was expected to occur in the Azores since the area is on the northernmost part of its range (Nafpaktitis *et al.,* 1977). MCZ material establishes this species for the Azores.

Azores Material. **109522,** R/V *Atlantis II* 49, RHB1916, 35°30′N 21°46′W, 39–41 m, 2229–0003 h, 24–25.VI.1969, 8:42–48 mm SL; **109523,** R/V *Atlantis II* 49, RHB1919, 35°56′N 22°40′W, 650–750 m, 0708–1030 h, 25.VI.1969, 3:40–43 mm SL; **109524,** R/V *Atlantis II* 49, RHB1920, 36°23′N 23°35′W, 63–65 m, 2045–2218 h, 25.VI.1969, 3:42–44 mm SL; **109591,** R/V *Chain* 105, RHB2551, 34°49′N 24°32′W, 700–740 m, 1620–1845 h, 08.VII.1972, 1:45 mm SL; **109592,** R/V *Chain* 105, RHB2552, 34°17′N 24°05′W, 60–70 m, 2158–2305 h, 08.VII.1972, 2:40–43 mm SL; **109671,** R/V *Delaware II* 63-04, DL63-04:012, 36°57′N 24°50′W, 180 m, 1730–1815 h, 12.V.1963, 1:42 mm SL.

Loweina rara (Lutken 1892)

Comments. L. rara is known from tropical areas of the Atlantic, Pacific, and Indian oceans (Nafpaktitis *et al.,* 1977; Bekker, 1983). In the Atlantic, the Azores is on the northern edges of its range. Hulley (1984) shows a locality near the Azores, which is confirmed by four stations in the MCZ material.

Azores Material. **102770,** R/V *Delaware II,* DL63-04:012, 36°57′N 24°50′W, 180 m, 1730–1815 h, 12.V.1963, 1:41 mm SL; **151184,** R/V *Atlantis II* 101, CEL7822, 39°41′N 32°19′W, 350–170–75 m, 2347–0140 h, 05–06.VII.1978, 2:41 mm SL; **151185,** R/V *Atlantis II* 101, CEL7823, 39°46′N 32°09′W, 350–175–75 m, 0150–0340 h, 06.VII.1978, 1:41 mm SL; **151186,** R/V *Atlan-*

tis II 101, CEL7829, 3/°54′N 27°22′W, 350–145 m, 0140–0340 h, 08.VII.1978, 1:39 mm SL.

Myctophum nitidulum Garman 1899

Comments. Occurs in the Indian, Pacific, and Atlantic oceans as a common tropical/subtropical species (Nafpaktitis *et al.*, 1977). Its presence in the area was expected, considering its distribution. The Azores is the northeastern edge of the species' range, but it does not appear to be common in the EEZ.

Azores Material. **106197,** R/V *Atlantis II* 49, SUN1921, 36°27′N 23°42′W, surface, 0000–0415 h, 25.VI.1969, 3:29–57 mm SL.

Notoscopelus caudispinosus (Johnson 1863)

Comments. Occurs in the Atlantic, Pacific, and Indian oceans. Questionably referred to a tropical/subtropical pattern (Nafpaktitis *et al.*, 1977). This species is more common in the western North Atlantic. The Azores represents the northern boundary in the eastern Atlantic, but it is apparently not common in the area.

Azores Material. **104073,** R/V *Chain* 105, RHB2552, 34°17′N 24°05′W, 60–70 m, 2158–2305 h, 08.VII.1972, 1:106 mm SL; **104093,** R/V *Chain* 105, RHB2554, 34°08′N 23°59′W, 480–520 m, 0115–0235 h, 09.VII.1972, 1:60 mm SL.

Melamphaidae

Scopelogadus mizolepis mizolepis (Günther 1878)

Comments. S. mizolepis is a bathypelagic species that inhabits the Atlantic, Pacific, and Indian oceans, but it was not previously known for the northeast Atlantic (Ebeling and Weed, 1963, 1973; Maul, 1973b, 1986). This subspecies is widespread in the western North Atlantic and in the eastern tropical Atlantic to South Africa (Ebeling and Weed, 1963, 1973; Ebeling, 1986; Maul, 1990). The juvenile specimens reported here from the western edge of the EEZ might well be waifs from the western Atlantic. Ebeling identified these specimens in 1963.

Azores Material. **42891,** R/V *Atlantis* Iselin, CODI/ATL119, 40°05′N 35°10′W, 1260–1440 m, ? h, 07.IX.1928, 2:19–24 mm SL.

Epigonidae

Microichthys coccoi Rüppell, 1852

Comments. Seven specimens of this rarely collected fish were caught in Azorean waters by the WHOI expeditions. It is interesting to note that these specimens were the only members of the genus *Microichthys* taken in thousands of WHOI trawls in the North Atlantic. The comparison of these juveniles and postlarvae with other epigonid specimens and illustrations shows that they do not belong to *Epigonus telescopus* since they lack the typical diagonal pigment slash on the caudal penducle. The MCZ specimens agree very closely with those figured as *Epigonus telescopus* in Kofoed (1952:1, pl. IIA; see Tortonese, 1986). Our records confirm this taxon in the Azores, but they are not the first for the area since all four specimens observed by Koefoed (1952) were caught at the EEZ.

Azores Material. **149630,** R/V *Atlantis II* 101, CEL7822, 39°41′N 32°19′W, 350–170 m, 2347–0140 h, 05–06.VII.1978, 1: 13 mm SL; **149629,** R/V *Atlantis II* 101, CEL7829, 37°54′N 27°22′W, 350–145 m, 0140–0340 h, 08.VII.1978, 1:21 mm SL; **149631,** R/V *Atlantis II* 101, CEL7834, 36°36′N 25°07′W, 350–170 m, 2355–0142 h, 09–10.VII.1978, 1:19 mm SL; **149632,** R/V *Atlantis II* 101, CEL7837, 37°48′N 23°39′W, 350 m, 2211–0045 h, 10–11.VI.1978, 2:17–20 mm SL; **149633,** R/V *Atlantis II* 101, CEL7838, 37°47′N 23°52′W, 350 m, 0045–0347 h, 11.VII.1978, 1:23 mm SL; **149634,** R/V *Atlantis II* 101, CEL7840, 38°49′N 22°20′W, 350–180 m, 2155–0047 h, 11–12.VII.1978, 1:18 mm SL.

CONCLUSION

The species reported here for the first time add about 5% to the total Azorean fish fauna and more than 15% to the known mesopelagic fishes (Santos *et al.*, 1997). The WHOI/MCZ Azorean collections represent more than 75% of all species known from the region and are certainly the most extensive documentation of mesopelagic fishes of the area.

The oceanic ichthyofauna of the Azores is primarily subtropical/temperate with a few species from subpolar cold water and warmer tropical waters. The archipelago is located at the boundary between temperate and subtropical water masses, since the Azores Front meanders through the area around the 35°N separating the two regions. The influence of the Azores Front on the biogeographic patterns of the Azores area has not been assessed. Backus *et al.* (1977), using collections of myctophids, created zoogeographic regions and provinces for the Atlantic. They include the Azores in the Azores–Britain Province of their North Atlantic Temperate Region. The definition of this province, however, raises some questions because faunistic and oceanographic gradients were observed throughout the area considered. Further evaluation of the role of mesoscale oceanographic structures as physical boundaries for mesopelagic fish will be of interest for the future development of an actual biogeographic model.

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Appendix 1. Data for the WHOI cruises in the Azorean EEZ.

Research Vessel	Date	Field No.	Lat.	Long.	Depth (m)	Day/Night
R/V *Atlantis*	9–14 July 1928	CODI/ATL001	39°58′ N	29°46′ W	Surface	No data
		CODI/ATL004	40°49′ N	30°24′ W	No data	No data
		CODI/ATL119	40°05′ N	35°10′ W	1,280–1,463	No data
R/V *Atlantis*	1931	ATLAN1931	37°47′ N	31°41′ W	No data	No data
R/V *Atlantis*	1947	ATLAN1947:015	35°37′ N	30°57′ W	3,200 mwo	No data
		ATLAN1947:816	35°37′ N	30° 51′ W	No data	No data
R/V *Atlantis*	1948	ATLAN1948:0818	37°50′ N	26°00′ W	2,520	No data
R/V Delaware II	14–17 May 1963	DL63-04:006	41°20′ N	29°20′ W	No data	No data
		DL63-04:012	36°57′ N	24°50′ W	180	No data
		DL63-04:013	37°25′ N	25°25′ W	Surface	No data
		DL63-04:014	37°25′ N	29°10′ W	No data	No data
		DL63-04:015	36°55′ N	32°32′ W	No data	No data
R/V *Atlantis II* Cr 13	20–27 Sept. 1964	RHB1036	42°20′ N	29°08′ W	470–520	D
		RHB1037	41°06′ N	29°19′ W	355–500	D
		RHB1038	41°03′ N	29°11′ W	350–450	D
		RHB1039	40°47′ N	28°41′ W	450–500	N
		RHB1040	36°27′ N	27°17′ W	320–375	D
		RHB1041	39°24′ N	27°11′ W	220–330	D
		RHB1042	38°04′ N	26°33′ W	025–035	N
		RHB1043	39°28′ N	31°00′ W	020–035	N
		RHB1044	39°37′ N	31°10′ W	200–475	N
		RHB1045	39°34′ N	33°37′ W	015–032	N
		SUN1043	39°28′ N	31°00′ W	Surface	N
		SUN1044	39°37′ N	31°10′ W	Surface	N
		SUN1045	39°34′ N	33°37′ W	Surface	N

Appendix 1. Continued.

Research Vessel	Date	Field No.	Lat.	Long.	Depth (m)	Day/Night
R/V *Atlantis II* Cr 49	24–27 June 1969	RHB1915	35°26′ N	21°39 W	063–067	N
		RHB1916	35°30′ N	21°46′ W	039–041	N
		RHB1917	35°34′ N	21°54′ W	135–140	N
		RHB1918	35°36′ N	22°05′ W	169–175	N
		RHB1919	35°56′ N	22°40′ W	650–750	D
		RHB1920	36°23′ N	23°35′ W	063–065	N
		RHB1921	36°27′ N	23°42′ W	105–110	N
		RHB1922	36°32′ N	23°49′ W	135–140	N
		RHB1923	36°36′ N	23°55′ W	240–250	N
		RHB1924	37°04′ N	24°42′ W	750–830	D
		RHB1925	37°57′ N	26°23′ W	032–034	N
		RHB1926	38°01′ N	26°25′ W	048–052	N
		RHB1927	38°07′ N	26°30′ W	120–125	N
		RHB1928	38°05′ N	26°29′ W	192–202	N
		SUN1915	35°26′ N	21°39′ W	Surface	N
		SUN1916	35°30′ N	21°46′ W	Surface	N
		SUN1917	35°34′ N	21°54′ W	Surface	N
		SUN1918	35°36′ N	22°05′ W	Surface	N
		SUN1920	36°23′ N	23°35′ W	Surface	N
		SUN1921	36°27′ N	23°42′ W	Surface	N
		SUN1922	36°32′ N	23°49′ W	Surface	N
		SUN1925	37°57′ N	26°23′ W	Surface	N
		SUN1926	38°01′ N	26°25′ W	Surface	N
		SUN1927	38°07′ N	26°30′ W	Surface	N
		SUN1928	38°05′ N	26°29′ W	Surface	N

Appendix 1. Continued.

Research Vessel	Date	Field No.	Lat.	Long.	Depth (m)	Day/Night
R/V *Chain* Cr 105	05–10 July 1972	RHB2535	42°26′ N	30°01′ W	060–065	N
		RHB2536	42°21′ N	30°00′ W	120–130	N
		RHB2537	42°17′ N	29°59′ W	225–255	N
		RHB2538	40°42′ N	29°15′ W	560–600	D
		RHB2540	39°55′ N	29°03′ W	060–070	N
		RHB2541	39°51′ N	29°00′ W	075–095	N
		RHB2542	39°47′ N	28°57′ W	165–175	N
		RHB2543	39°10′ N	28°33′ W	250–260	N–D
		RHB2544	37°28′ N	26°38′ W	070–075	N
		RHB2546	37°20′ N	26°30′ W	200–320	N
		RHB2547	36°21′ N	25°39′ W	700–760	D
		RHB2548	35°14′ N	24°41′ W	070–075	N
		RHB2549	35°08′ N	24°25′ W	040–045	N
		RHB2550	35°03′ N	24°30′ W	290–310	N
		RHB2551	34°49′ N	24°32′ W	700–740	D
		RBH2552	34°17′ N	24°05′ W	060–070	N
		RHB2553	34°12′ N	24°01′ W	125–135	N
		RHB2554	34°08′ N	23°59′ W	480–520	N
		RHB2555	34°00′ N	22°55′ W	470–520	D
		SUN2535	42°26′ N	30°01′ W	Surface	N
		SUN2536	42°21′ N	30°00′ W	Surface	N
		SUN2537	42°17′ N	29°59′ W	Surface	N
		SUN2540	39°55′ N	29°03′ W	Surface	N
		SUN2541	39°51′ N	29°00′ W	Surface	N
		SUN2544	37°28′ N	26°38′ W	Surface	N
		SUN2545	37°23′ N	26°33′ W	Surface	N

APPENDIX 1. CONTINUED.

Research Vessel	Date	Field No.	Lat.	Long.	Depth (m)	Day/Night
		SUN2546	37°20′ N	26°30′ W	Surface	N
		SUN2548	35°14′ N	24°41′ W	Surface	N
		SUN2549	35°08′ N	24°25′ W	Surface	N
		SUN2552	34°17′ N	24°05′ W	Surface	N
R/V *Atlantis II* Cr 78	05 Sept. 1973	RHB2900	37°09′ N	26°06′ W	520–000	N
R/V *Atlantis II* Cr 101	05–10 July 1978	CEL7818	40°50′ N	34°11′ W	1,000	N
		CEL7819	40°12′ N	34°04′ W	800	N
		CEL7820	40°14′ N	33°02′ W	40–20	D
		CEL7821	39°41′ N	32°19′ W	200–090	N
		CEL7822	39°41′ N	32°19′ W	350-170-75	N
		CEL7823	39°46′ N	32°09′ W	350-175-75	N
		CEL7824	38°59′ N	31°38′ W	35–12	D
		CEL7825	38°59′ N	30°39′ W	350–220	N
		CEL7826	38°59′ N	30°32′ W	400–220	N
		CEL7827	37°51′ N	27°33′ W	120-40-60	N
		CEL7828	37°51′ N	27°33′ W	120-40-60	N
		CEL7829	37°54′ N	27°22′ W	350–145	N
		CEL7830	35°55′ N	25°55′ W	40	D
		CEL7831	36°37° N	25°03′ W	350–190	N
		CEL7832	36°36′ N	25°07′ W	350–190	N
		CEL7833	36°37′ N	25°04′ W	350-170-80	N
		CEL7834	36°36′ N	25°07′ W	350-170-80	N
		CEL7835	36°38′ N	25°18′ W	350-170-180	N
		CEL7836	37°08′ N	24°25′ W	10–40	D
		CEL7837	37°48′ N	23°39′ W	350	N

Appendix 1. Continued.

Research Vessel	Date	Field No.	Lat.	Long.	Depth (m)	Day/Night
		CEL7838	37°47′ N	23°52′ W	350	N
		CEL7839	38°21′ N	23°00′ W	40	D
		CEL7840	38°49′ N	22°20′ W	35-180-190	N
		CEL7841	38°44′ N	22°09′ W	350-180-190	N
R/V *Oceanus* Cr 158	25 Aug–2 Sept 1984	KEH8475	37°37′ N	32°55′ W	060 mwo	N
		KEH8476	37°37′ N	32°55′ W	400 mwo	N
		KEH8477	37°35′ N	32°55′ W	600 mwo	N
		KEH8478	37°33′ N	32°54′ W	050 mwo	N
		KEH8479	39°05′ N	31°21′ W	400 mwo	N
		KEH8480	39°05′ N	31°21′ W	1,000 mwo	N
		KEH8481	39°01′ N	31°20′ W	500 mwo	N
		KEH8482	38°58′ N	31°22′ W	030 mwo	N
		KEH8483	38°57′ N	31°22′ W	600 mwo	N
		KEH8484	38°55′ N	31°21′ W	500 mwo	N
		KEH8485	38°32′ N	30°06′ W	1,500 mwo	N
		KEH8486	38°30′ N	30°09′ W	1,500 mwo	N
		KEH8487	38°11′ N	29°38′ W	400 mwo	N
		KEH8488	38°10′ N	29°39′ W	1,500 mwo	N
		KEH8489	38°06′ N	29°44′ W	400 mwo	N
		KEH8490	38°04′ N	26°57′ W	2,000 mwo	N

Appendix 2. Deep sea fish species from the Azores EEZ in the Museum of Comparative Zoology. Species reported in the previous sections as new to area not included in this appendix. C, number of collection; S, number of specimens; R, size range (mm SL); D, developmental stage; larvae (L) and juveniles and adults (A).

Family	Species	C	S	R	D	MCZ catalog number and field number
Notacanthidae	*Tiluropsis* sp.	1	1	307	L	88684, KEH8477.
Nemichthyidae	*Nemichthys curvirostris*	1	1	500	A	149501, CEL7832.
	Nemichthys scolopaceus	11	18	310-757	L, A	73846, CEL7827; 73847, CEL7828; 73848, CEL7831; 73849, CEL7832; 149619, CEL7834; 150939, CEL7838; 149611, CEL7840; 147253, RHB2537; 147249, RHB2544; 147275, RHB2546; 73832, RHB2547.
Congridae	*Conger conger*	5	5	78-119	L	71801, CEL7821; 71802, CEL7827; 71803, CEL7828; 85078, KEH8482; 71790, RHB2549.
Nettastomatidae	*Facciolella oxyrhynclius*	2	2	124-155	L	65337, CEL7835; 65341, RHB1916.
	Nettastoma melanura	3	3	36-102	L	60627, RHB1917; 65437, RHB2549; 65445, RHB2550.
Serrivomeridae	*Serrivomer beanii*	2	2	120	A	65858, RHB2552; 65550, RHB25505.
	Serrivomer lanceolatoides	1	1	410	A	149511, CEL7818.
Cyematidae	*Cyema atrum*	4	5	42	L	73935, CEL7832; 73929, RHB2553; 60597, RHB 2551; 60600, RHB2554.
Microstomatidae	*Microstoma microstoma*	2	2	20-79	L, A	66001, RHB2553; 66009, RHB1041.
Opisthoproctidae	*Opisthoproctus grimaldii*	5	6	18-50	L, A	66380, RHB1039; 66390, RHB1041; 66386, RHB1924; 66385, RHB2550; 66417, RHB2555.
	Opisthoproctus soleatus	6	12	18-36	L, A	66265, RHB1036; 66405, RHB1038; 61958, RHB1039; 66398, RHB1919; 66397, RHB1924; 66422, RHB2555.
Alepocephalidae	*Bathytroctes microlepis*	1	1	157	A	040599, ATLAN1948:0818.
	Xenodermichthys copei	1	2	41-49	A	128285, RHB2547.
Platytroctidae	*Holtbyrnia* sp.	2	2	16-20	L	128249, RHB1919; 75472, RHB1924.
	Searsia koefoedi	1	1	25	A	100986, RHB1039.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
Gonostomatidae	*Bonapartia pedaliota*	11	32	15-50	L A	87335, KEH8478; 79892, KEH8483; 79893, KEH8484, 79874, RHB1036; 144629, RHB1037, 144630, RHB1038, 58629, RHB1039, 144631, RHB1041; 79876, RHB1923; 144700, RHB2550; 144701, RHB2554.
	Cyclothone alba	2	2	19-23	A	144142, RHB1036; 144143, RHB1039.
	Cyclothone braueri	7	600	10-31	A	151178, CEL7837; 151304, CEL7840; 143445, RHB1036; 143371, RHB1039; 143372, RHB1041; 143438, RHB1919; 143416, RHB1924.
	Cyclothone microdon	4	64	12-45	A	150980, CEL7818; 143066, RHB1040; 143078, RHB1919, 143079, RHB1924
	Cyclothone pallida	2	3	29-34	A	142691, RHB1036; 142707, RHB1919.
	Gonostoma bathyphilum	1	4	22-24	L	149544, KEH8485.
	Gonostoma denudatum	10	26	18-60	L A	150896, CEL7818; 150897, CEL7822; 150898, CEL7827; 150899, CEL7828; 150900, CEL7829; 149493, CEL7837; 141752, RHB1045; 141772, RHB1927; 80052, RHB2543; 141785, RHB2549.
	Gonostoma elongatum	12	26	15-215	A	141700, ATLAN1948:0818; 149533, CEL7818; 149531, CEL7826; 149530, CEL7831; 149527, CEL7832; 150945, CEL7833; 149528, CEL7838; 141353, RHB1039; 141547, RHB1917; 141298, RHB2537; 141352, RHB2546; 141355, RHB2550; 141299, RHB2553.
	Margrethia obtusirostra	7	7	15-52	L A	149549, CEL7826; 87358, KEH8479; 87359, KEH8480; 96940, RHB1041; 89271, RHB2546; 89287, RHB2550; 89288, RHB2553.
Sternoptychidae	*Argyropelecus aculeatus*	27	114	10-60	A	31631, CODI/ATL004; 137858, DL63-04:012; 150941, CEL7818; 150949, CEL7822; 150962, CEL7822; 150963, CEL7825; 150953, CEL7826; 150951, CEL7829; 150955, CEL7831; 150950, CEL7832; 150954, CEL7832; 150956, CEL7833; 150964, CEL7834; 150965, CEL7835; 150966, CEL7837; 150967, CEL7838; 137459, RHB1044, 137805, RHB1915; 137458, RHB1918; 137660, RHB1919, 137819, RHB1922; 137661, RHB1923; 137825, RHB2546; 137688, RHB2547; 137808, RHB2552; 137469, RHB2555; 137848, SUN1915.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Argyropelecus hemigymnus	31	576	6-36	A	150958, CEL7818; 150985, CEL7822; 150986, CEL7825; 150987, CEL7826; 150988, CEL7827; 150989, CEL7832; 150990, CEL7838; 150984, KEH8485; 150957, KEH8489; 137056, RHB1036; 136261, RHB1037; 135838, RHB1038; 135815, RHB1039; 136918, RHB1039; 136262, RHB1044; 136332, RHB1919; 136333, RHB1924; 66657, RHB2537; 136434, RHB2538; 135827, RHB2540; 136435, RHB2541; 136436, RHB2542; 135825, RHB2546; 136437, RHB2547; 136438, RHB2548; 136439, RHB2550; 136440, RHB2551; 136441, RHB2552; 135819, RHB2554; 136442, RHB2555; 136472, RHB2900.
	Argyropelecus olfersi	12	15	10-48	A	31634, CODI/ATL004; 75511, CEL7841; 150935, RHB1037; 135728, RHB1037, 135729, RHB1038; 45291, RHB1039; 135730, RHB1040; 135737, RHB1040; 135731, RHB1919; 135738, RHB1923; 135732, RHB2536; 135739, RHB2542
	Maurolicus muelleri / *Maurolicus amestinopunctatus*	9	30	12-32	A	92552, RHB1039; 92495, RHB1922; 92496, RHB1927; 92497, RHB1928; 92486, RHB2536; 92510, RHB2540; 92511, RHB2541; 92512, RHB2542; 92513, RHB2550.
	Sternoptyx diaphana	1	1	28	A	135218, DL63-04:015,1.
	Valenciennellus tripunctulatus	19	117	18-29	L A	150903, CEL7818; 87349, KEH8477; 87350, KEH8485; 150905, KEH8485; 150906, KEH8489; 133808, RHB1038; 133809, RHB1039; 81446, RHB1041; 133874, RHB1919; 133875, RHB1923; 133876, RHB1924; 133936, RHB2546; 133937, RHB2547; 133938, RHB2551; 133939, RHB2554; 66691, RHB2555; 133705, RHB2555, 133949, RHB2900; 133807, RHB1036.
Photichthyidae	*Ichthyococcus ovatus*	4	5	16-37	A	140622, RHB1038; 140623, RHB1039; 90874, RHB2550; 90873, RHB2555.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Vinciguerria attenuata	27	270	12-43	L A	80907, KEH8483; 80908, KEH8486; 139479, RHB1038; 80845, RHB1036; 139478, RHB1036; 139480, RHB1039; 80846, RHB1041; 139481, RHB1041; 80847, RHB1043; 139482, RHB1044, 80848, RHB1045; 139547, RHB1919; 80880, RHB1926; 139625, RHB2535; 139626, RHB2536; 139627, RHB2537; 139628, RHB2542; 139629, RHB2547; 80895, RHB2548; 139630, RHB2548; 139631, RHB2551; 80896, RHB2552; 139632, RHB2552; 80897, RHB2553; 80898, RHB2554, 139633, RHB2554; 139634, RHB2555.
	Vinciguerria nimbaria	3	3	25-39	A	139209, RHB1915; 139210, RHB1920; 139211, RHB1921.
	Vinciguerria poweriae	22	144	14-38	L A	87369, KEH8479; 87370, KEH8480; 87371, KEH8484; 138106, KEH8484, 80935, RHB1045; 138334, RHB1915; 138335, RHB1917; 138336, RHB1921; 138337, RHB1922; 138338, RHB1923; 138339, RHB1927; 138340, RHB1928; 138457, RHB2535; 138458, RHB2540; 138459, RHB2544; 138460, RHB2548; 138461, RHB2549; 138462, RHB2550; 80982, RHB2552; 138463, RHB2552; 138464, RHB2553; 138465, RHB2554.
Stomiidae	*Aristostomias tittmani*	1	1	77	A	149494, CEL7832.
	Astronesthes niger	16	55	25-82	A	149510, CEL7840; 133146, SUN1917; 133110, SUN2535; 133198, SUN2535; 133111, SUN2536; 133199, SUN2536; 133112, SUN2540; 133113, SUN2540; 133200, SUN2540; 133201, SUN2541; 133202, SUN2545; 133203, SUN2546; 133204, SUN2546; 133205, SUN2546; 133206, SUN2552; 133207, SUN2552.
	Bathophilus nigerrimus	1	1	56	A	149509, CEL7840
	Bathophilus vaillanti	13	19	34-113	A	149540, CEL7835; 149541, CEL7838; 84948, RHB2549; 84949, RHB2554; 84813, RHB1036; 84809, RHB1043; 84812, RHB1918; 84816, RHB1919; 84827, RHB1920; 84828, RHB1921; 84829, RHB1922; 84830, RHB1927; 84831, RHB1928.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Chauliodus danae	15	40	21-120	A	151016, CEL7826; 151018, CEL7831; 151017, CEL7832; 129247, RHB1917; 55129, RHB1918, 129246, RHB1919; 55116, RHB1922; 129241, RHB1923; 131197, RHB2540; 131198, RHB2546; 58784, RHB2548; 129221, RHB2550, 129208, RHB2551; 129224, RHB2552; 131199, RHB2554.
	Chauliodus sloani	25	79	21-162	A	151021, CEL7818; 151022, CEL7822; 151014, CEL7829; 151025, CEL7832; 151023, CEL7833; 151015, CEL7835; 151024, CEL7837; 150938, CEL7838; 129353, RHB1036; 129282, RHB1041; 129318, RHB1044; 130156, RHB1919; 130157, RHB1921; 130158, RHB1927; 130227, RHB2535, 129329, RHB2536, 129339, RHB2537; 129293, RHB2538; 129325, RHB2540; 130228, RHB2546; 130229, RHB2547; 130230, RHB2549; 130231, RHB2551; 130232, RHB2555, 129094, RHB2900.
	Chirostomias pliopterus	3	3	40-60	A	149608, CEL7834; 132712, RHB1928, 132715, RHB2549.
	Idiacanthus fasciola	10	24	78-302	A	149519, CEL7822; 149524, CEL7826; 149520, CEL7831; 149522, CEL7840; 89619, RHB1921; 89582, RHB1927; 89769, RHB2548, 89803, RHB2550; 89764, RHB2553; 89804, RHB2555.
	Leptostomias gladiator	1	1	112	A	149495, CEL7837.
	Malacosteus niger	2	2	49-110	A	131795, RHB1919; 131810, RHB2547.
	Photonectes margarita	1	1	121	A	149508, CEL7840.
	Photostomias guernei	6	10	50-101	A	149516, CEL7825; 149515, CEL7826; 149514, CEL7832, 149610, KEH8488; 131646, RHB1918; 131647, RHB1919.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Stomias boa	26	150	30-132	A	151033, CEL7818; 151034, CEL7822; 151035, CEL7827; 151036, CEL7833, 151029, CEL7835; 151037, CEL7835; 151030, CEL7837; 151031, CEL7838; 150942, CEL7840; 129798, RHB1043; 95508, RHB1045; 129808, RHB1915; 129809, RHB1926; 129810, RHB1927; 129811, RHB1928; 129828, RHB2535; 129037, RHB2536; 129829, RHB2536; 95529, RHB2537; 129830, RHB2537; 129831, RHB2538; 129832, RHB2540; 95530, RHB2541; 129833, RHB2542; 129834, RHB2543; 129835, RHB2547.
Bathypteroidae	*Bathypterois longipes*	1	1	147	A	36634, ATLAN4715.
Scopelarchidae	*Benthalbella infans*	6	18	35-49	L	150937, CEL7818; 70319, KEH8490; 70340, RHB1037; 70317, RHB1038; 70318, RHB2555; 70329, RHB2900.
	Scopelarchus analis	12	15	13-71	L A	150879, CEL7822; 150880, CEL7831; 150799, CEL7834, 150881, CEL7835; 69269, RHB1036; 69331, RHB1921; 69332, RHB1923; 69333, RHB1928; 69403, RHB2546; 69404, RHB2549; 69405, RHB2551; 69406, RHB2553.
Notosudidae	*Ahliesaurus berryi*	1	1	81	A	15934, CEL7825.
	Scopelosaurus lepidus	7	10	41-45	L A	150926, CEL7822; 150927, CEL7838; 150928, CEL7840; 83689, RHB2535, 126960, RHB2536; 126961, RHB2537; 126962, RHB2542.
Paralepididae	*Arctozenus rissoi*	15	29	19-72	L	68774, RHB1036; 68775, RHB1038; 68776, RHB1039; 68777, RHB1044; 67794, RHB1045; 68792, RHB1918; 68814, RHB1924; 67577, RHB2538; 67578, RHB2542; 67579, RHB2543; 67580, RHB2547; 67581, RHB2548; 67582, RHB2551; 67583, RHB2553; 67609, RHB2900.
	Lestidiops jayakari	4	6	24-69	L	68985, RHB1036; 68073, RHB1038; 68074, RHB1039; 68075, RHB1045
	Lestidiops sphyrenoides	3	5	31-49	L	68952, RHB1924, 68953, RHB1926; 68954, RHB1927.
	Paralepis atlantica	1	1	98	A	68708, DL63-04:015.
	Paralepis coregonoides	6	16	10-21	L A	43146, DL63-04:006; 43143, DL63-04:014; 128199, RHB1919; 68716, RHB1036; 68744, RHB1037; 68717, RHB1039; 68746, RHB1927.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Sudis hyalina	1	1	8	L	68570, RHB1043.
Evermannellidae	*Evermannella balbo*	11	25	13-33	L A	150882, CEL7828; 150883, CEL7829; 150884, CEL7831; 73191, KEH8476; 73192, KEH8477; 73193, KEH8479; 73194, KEH8483; 73195, KEH8484; 73196, KEH8485; 52336, RHB1041; 52321, RHB1045.
Omosudidae	*Omosudis lowei*	1	1	8	L	69246, RHB1036.
Alepisauridae	*Alepisaurus brevirostris*	1	1	98	A	127289, DL63-04:015.
Myctophidae	*Benthosema glaciale*	18	975	9-44	A	150996, CEL7823; 150997, CEL7835; 150998, CEL7837; 150999, CEL7838; 151000, CEL7840; 150996, CEL7823; 126015, RHB1039; 126016, RHB1045; 126036, RHB1920; 126037, RHB1924; 125920, RHB2535, 126068, RHB2536, 126069, RHB2537; 126070, RHB2538; 126071, RHB2540; 126072, RHB2541; 126073, RHB2544, 126102, RHB2900.
	Benthosema suborbitale	14	70	11-29	A	150991, CEL7825; 150992, CEL7828; 150993, CEL7831; 150994, CEL7837; 150995, CEL7838; 125384, RHB1916; 125385, RHB1920; 125429, RHB2547; 125430, RHB2549; 125431, RHB2550; 125432, RHB2551; 125433, RHB2552; 125434, RHB2553; 125435, RHB2554.
	Bolinichthys indicus	29	84	29-45	A	151003, CEL7818; 151004, CEL7822; 151005, CEL7826; 151006, CEL7831; 151007, CEL7833; 151008, CEL7834; 151009, CEL7835; 151010, CEL7837; 151011, CEL7838, 151012, CEL7840; 151013, CEL7841; 151002, KEH8489; 33259, CODI/ATL119; 124444, RHB1919; 124445, RHB1924; 124446, RHB1927; 124561, RHB2535; 124562, RHB2536; 124563, RHB2540; 124564, RHB2541; 124565, RHB2542; 124566, RHB2544, 124567, RHB2547, 124568, RHB2548; 124569, RHB2549; 124570, RHB2550; 124571, RHB2551; 124572, RHB2552; 124573, RHB2553; 124574, RHB2554.

Appendix 2. Continued.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Ceratoscopelus maderensis	31	613	15-64	A	151038, CEL7818, 151040, CEL7825, 151212, CEL7826; 151213, CEL7826, 151041, CEL7827, 151042, CEL7828; 151043, CEL7831; 151044, CEL7832; 151302, CEL7833; 151045, CEL7837; 151046, CEL7840; 151303, CEL7840, 122809, RHB1036; 122810, RHB1039; 122811, RHB1040; 122812, RHB1041, 122701, RHB1042; 122702, RHB1043; 122813, RHB1044; 122814, RHB1045, 122859, RHB1928; 122906, RHB2535; 122907, RHB2540; 122908, RHB2541, 122909, RHB2546; 122910, RHB2547; 122911, RHB2549; 122912, RHB2550; 122913, RHB2551; 122914, RHB2552; 55531, RHB2900.
	Ceratoscopelus warmingii	9	36	22-63	A	151145, CEL7831; 122234, RHB1920; 121755, RHB1922; 122315, RHB2548; 122316, RHB2549; 122317, RHB2550; 121764, RHB2552; 122318, RHB2553; 122319, RHB2554.
	Diaphus effulgens	2	2	65	A	49172, RHB2538; 110137, RHB2550.
	Diaphus holti	19	57	11-46	A	151049, CEL7822; 151050, CEL7825; 151051, CEL7826; 151052, CEL7829, 151053, CEL7832; 151054, CEL7833; 151055, CEL7838, 120635, DL63-04:012; 120478, RHB1036; 120479, RHB1038; 120480, RHB1039; 120481, RHB1041; 120482, RHB1045, 120505, RHB1923; 120613, RHB2536; 120614, RHB2537, 120615, RHB2542; 120616, RHB2549; 120617, RHB2552.
	Diaphus metopoclampus	5	6	25-74	A	151057, CEL7826, 151058, KEH8485; 120039, RHB1039; 120049, RHB1923; 120067, RHB2550.
	Diaphus mollis	5	10	37-48	A	149628, CEL7831; 119798, RHB2547; 119799, RHB2548; 119800, RHB2553; 119801, RHB2554.

Appendix 2. Continued.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Diaphus rafinesquii	36	117	29-75	A	151062, CEL7818; 151068, CEL7822; 151061, CEL7823; 151063, CEL7829; 151069, CEL7831; 151064, CEL7832; 151070, CEL7833, 151066, CEL7834; 151071, CEL7835; 151059, CEL7837; 151060, CEL7838; 151072, CEL7840; 151073, CEL7841; 151074, KEH8485; 151067, KEH8489; 118625, RHB1036; 118626, RHB1039; 118627, RHB1041; 118628, RHB1044, 118830, RHB1919; 118831, RHB1927; 118904, RHB2536; 118905, RHB2537; 118906, RHB2538; 118658, RHB2540; 118907, RHB2541; 118908, RHB2542; 118909, RHB2544, 118910, RHB2546; 118911, RHB2548; 118912, RHB2550; 118913, RHB2551, 118914, RHB2553; 118915, RHB2554; 118916, RHB2555; 118660, RHB2900.
	Diogenichthys atlanticus	25	350	6-23	A	151105, CEL7822; 151106, CEL7823; 151107, CEL7827; 151108, CEL7828; 151109, CEL7829, 151110, CEL7834; 151111, CEL7835; 151112, CEL7838; 118091, DL63-04:012; 117731, RHB1039; 117732, RHB1044; 117733, RHB1045; 117835, RHB1920; 55530, RHB1926; 117957, RHB2535; 117958, RHB2544; 117959, RHB2546; 117960, RHB2547; 117961, RHB2548; 117962, RHB2549; 117963, RHB2550; 117964, RHB2551; 117965, RHB2552; 117966 RHB2553, 117967, RHB2554.
	Electrona rissoi	20	206	4-43	A	151094, CEL7818; 151095, CEL7825; 151096, CEL7826; 151097, CEL7829; 151098, CEL7831; 151099, CEL7832; 151100, CEL7833, 151101, CEL7838; 151102, CEL7840; 151103, CEL7841; 151104, KEH8489; 103048, RHB1036; 103049, RHB1038; 62188, RHB1039; 103050, RHB1041; 103051, RHB1044; 103061, RHB1928; 103074, RHB2543; 103075, RHB2546; 103076, RHB2550.

Appendix 2. Continued.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Gonichthys coccoi	54	649	8-58	L A	151088, CEL7822; 151089, CEL7827; 151090, CEL7828; 151091, CEL7835; 151092, CEL7837; 109966, DL63-04:012; 117340, DL63-04:013; 116502, RHB1036; 116525, RHB1927; 116559, RHB2538; 116560, RHB2552, 116604, SUN1043; 116793 SUN1044; 116605, SUN1045; 116677, SUN1915; 116883, SUN1915; 116884, SUN1916; 116885, SUN1916; 116678, SUN1917; 116679, SUN1918; 116680, SUN1920; 116681, SUN1920; 116886, SUN1921; 116887, SUN1921; 116888, SUN1922; 116889, SUN1925; 116890, SUN1925; 116891, SUN1926, 116892, SUN1926; 116893, SUN1926; 116894, SUN1927; 116895, SUN1927; 116682, SUN1928; 116957, SUN2535; 116958, SUN2535, 116959, SUN2535; 116960, SUN2536; 116961, SUN2536; 116962, SUN2537; 116963, SUN2537; 116964, SUN2537, 116704, SUN2540; 116965, SUN2540; 116966, SUN2540; 116967, SUN2541; 116968, SUN2544; 116969, SUN2545; 116970, SUN2545; 116971, SUN2545; 116972, SUN2546; 116973, SUN2546, 116974, SUN2546; 116975, SUN2548; 116976, SUN2552.
	Hygophum benoiti	16	258	7-45	A	151209, KEH8485; 116232, RHB1036; 116233, RHB1039; 116234, RHB1043, 116235, RHB1044; 116277, RHB1915; 116278, RHB1916; 116279, RHB1919; 115997, RHB1920; 116280, RHB1923; 116281, RHB1924; 116282, RHB1927; 116317, RHB2544; 116318, RHB2547; 116319, RHB2548; 116320, RHB2551
	Hygophum hygomii	30	129	16-57	A	151075, CEL7823; 151076, CEL7827; 151077, CEL7828; 151078, CEL7833; 151079, CEL7834; 151080, CEL7835; 151081, CEL7838; 151082, CEL7841; 115791, DL63-04:012; 115846, RHB1043; 115847, RHB1044; 115848, RHB1045; 115738, RHB1915; 115739, RHB1916; 115899, RHB1919; 115740, RHB1920; 115900, RHB1923; 115901, RHB1924; 115741, RHB1926; 115929, RHB2546; 115930, RHB2547; 115931, RHB2549; 115932, RHB2551; 115933, RHB2552; 115626, SUN1918; 115631, SUN2535; 115632, SUN2544; 115633, SUN2545; 115634, SUN2546; 115635, SUN2549.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Lampadena chavesi	2	2	35-61	A	103095, RHB1044; 103114, RHB2554.
	Lampadena speculigera	9	24	21-38	A	151084, CEL7823; 151210, CEL7826; 151085, CEL7834; 151086, CEL7837; 151087, CEL7838; 114345, RHB2540; 114346, RHB2541; 114347, RHB2542; 114348, RHB2551.
	Lampanyctus ater	25	87	35-103	A	151187, CEL7822; 151310, CEL7823; 151196, CEL7825; 151188, CEL7826; 151197, CEL7829; 151171, CEL7831; 151189, CEL7832; 151190, CEL7833; 151311, CEL7834; 151312, CEL7837; 151313, CEL7840; 113452, DL63-04:012; 151309, KEH8485; 113371, RHB1921; 113510, RHB1922; 113372, RHB1923; 113373, RHB1927; 113524, RHB2536; 113398, RHB2537; 113399, RHB2540; 113400, RHB2541; 113401, RHB2542; 113402, RHB2544; 113403, RHB2551; 113404, RHB2553.
	Lampanyctus crocodilus.	27	409	18-38	A	151315, CEL7818; 151191, CEL7822; 151316, CEL7823, 151192, CEL7825; 151193, CEL7826; 151317, CEL7827; 151194, CEL7829; 151195, CEL7833; 151319, CEL7834; 151259, CEL7835; 151320, CEL7837; 151321, CEL7838; 151322, CEL7840; 151323, CEL7841; 151314, KEH8485; 113284, RHB1924; 113216, RHB2536; 113217, RHB2537; 113218, RHB2540; 113314, RHB2541; 113315, RHB2542; 113316, RHB2544; 113317, RHB2547, 113318, RHB2548; 113319, RHB2549; 113320, RHB2552; 113321, RHB2554
	Lampanyctus festivus	2	3	64-76	A	151208, CEL7831 158261, CEL7832.
	Lampanyctus intricarius.	17	184	26-68	A	151325, CEL7818; 151326, CEL7823; 151327, CEL7827; 151207, CEL7833, 151328, CEL7834; 151260, CEL7835; 151329, CEL7837; 151330, CEL7838, 151331, CEL7840; 151332, CEL7841; 112384, DL63-04:012; 112355, RHB2536; 151324, KEH8485; 112356, RHB2537; 112369, RHB2540; 112370, RHB2541, 112357, RHB2542.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Lampanyctus photonotus	13	39	47-64	A	151307, CEL7823; 151204, CEL7825; 151205, CEL7826; 151308, CEL7827; 111907, RHB1043; 112019, RHB2540; 112020, RHB2544; 111848, RHB2548; 112021, RHB2549; 112022, RHB2550; 111849, RHB2552; 111850, RHB2553; 112031, RHB2900.
	Lampanyctus pusillus	47	732	14-40	A	151334, CEL7818; 151198, CEL7822; 151335, CEL7823; 151199, CEL7825, 151200, CEL7826; 151336, CEL7827; 151201, CEL7829; 151262, CEL7831; 151202, CEL7832; 151203, CEL7833; 151338, CEL7834, 151263, CEL7835; 151339, CEL7837; 151340, CEL7838; 151341, CEL7840; 151342, CEL7841; 151333, KEH8485; 151264, KEH8489; 33267, CODI/ATL119; 111535, DL63-04:012; 111271, RHB1036; 110934, RHB1039; 111272, RHB1043; 111273, RHB1044; 110935, RHB1045; 111345, RHB1915; 111346, RHB1918; 111347, RHB1919; 111348, RHB1923; 111349, RHB1924; 111350, RHB1927; 110961, RHB1928; 110976, RHB2535; 111477, RHB2536; 111478, RHB2537; 110977, RHB2540; 111479, RHB2541; 111480, RHB2542; 111481, RHB2544; 111482, RHB2546; 111483, RHB2547; 110978, RHB2548; 111484, RHB2549; 111485, RHB2550; 111486, RHB2551; 110979, RHB2552; 111487, RHB2554, 111516, RHB2900.
	Lepidophanes guentheri	1	1	53	A	108641, RHB1044.

Appendix 2. Continued.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Lobianchia dofleini	48	639	6-40	A	151114, CEL7818; 151115, CEL7822; 151125, CEL7823; 151116, CEL7826; 151117, CEL7827; 151118, CEL7828; 151119, CEL7829; 151120, CEL7831; 151121, CEL7832; 151128, CEL7833; 151122, CEL7834; 151123, CEL7835, 151126, CEL7837; 151127, CEL7838; 151129, CEL7840; 151124, CEL7841; 151113, KEH8485; 107995, DL63-04:012; 107718, RHB1036; 107617, RHB1038; 107719, RHB1041; 107720, RHB1042, 107721, RHB1043; 107722, RHB1044, 107723, RHB1045; 107801, RHB1915, 107802, RHB1916, 107661, RHB1920; 107803, RHB1921; 107804, RHB1923; 107805, RHB1924; 107806, RHB1927, 107919, RHB2535; 107920, RHB2536; 107921, RHB2540; 107922, RHB2541; 107923, RHB2544; 107924, RHB2546; 107925, RHB2547; 107926, RHB2548, 107927, RHB2549; 107928, RHB2550; 107929, RHB2551; 107930, RHB2552; 107685, RHB2553, 107931, RHB2554; 107932, RHB2555, 107954, RHB2900.
	Lobianchia gemellarii	12	19	27-43	A	151130, CEL7825; 151131, CEL7831; 151132, CEL7834; 107136, RHB1038; 107137, RHB1044; 107233, RHB1921; 107234, RHB1922; 107235, RHB1923; 107286, RHB2541; 107287, RHB2544; 107288, RHB2547; 107289, RHB2550
	Loweina interrupta	2	3	24-28	A	151179, CEL7823; 149505, CEL7837.
	Myctophum punctatum	29	192	19-79	A	151134, CEL7818; 151135, CEL7822; 151136, CEL7823; 151137, CEL7826; 151138, CEL7828; 151139, CEL7833; 151140, CEL7834; 151146, CEL7837; 151141, CEL7838; 151142, CEL7840; 151143, CEL7841; 49552, DL63-04:012; 105666, DL63-04:013; 105424, RHB1039; 105484, RHB1926; 105454, RHB2540; 105520, SUN1043; 105618, SUN1044; 105619, SUN1045; 105547, SUN1918; 105638, SUN1920; 105550, SUN1925, 105525, SUN1926; 105542, SUN2535; 105493, SUN2536; 105496, SUN2540; 105545, SUN2540; 105505, SUN2544.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
	Notolychnus valdiviae	25	249	15-25	A	151147, CEL7818; 151148, CEL7823; 151149, CEL7825; 151211, CEL7826; 151150, CEL7832; 151151, CEL7833; 151152, CEL7834; 151153, CEL7835, 151154, CEL7837; 151155, CEL7838; 151156, CEL7841; 104818, RHB1036; 104819, RHB1039; 104820, RHB1041; 104821, RHB1045; 104919, RHB1915; 105067, RHB2538, 105068, RHB2540; 105069, RHB2541; 105070, RHB2542; 105071, RHB2544, 105072, RHB2548; 105073, RHB2549; 105074, RHB2552; 105075, RHB2553.
	Notoscopelus bolini	14	33	26-103	A	151158, CEL7822; 151159, CEL7823; 151160, CEL7833; 151161, KEH8485; 151162, KEH8489; 104021, RHB1915; 104022, RHB1916; 104023, RHB1920; 104024, RHB1925; 104025, RHB1926; 104026, RHB1927, 104031, RHB2540; 104032, RHB2541; 103997, RHB2546.
	Notoscopelus elongatus	1	1	27	A	104268, RHB2537.
	Notoscopelus resplendens	18	129	8-67	L A	151163, CEL7831; 151164, CEL7835; 151165, CEL7841; 103732, DL63-04:012; 103822, RHB1044; 103786, RHB1915; 103876, RHB1916; 103877, RHB1917; 103787, RHB1920; 103878, RHB1921; 103879, RHB1922; 103788, RHB1926; 103948, RHB2544; 103802, RHB2548; 103949, RHB2549; 103803, RHB2552; 103950, RHB2553; 103958, RHB2900.
	Protomyctophum arcticum	1	1	15	A	103011, RHB1039.
	Symbolophorus veranyi	17	29	25-111	A	151166, CEL7822; 151170, CEL7826; 151167, CEL7829; 151168, CEL7837; 151169, CEL7838; 103390, RHB1039; 103246, RHB1045; 103400, RHB1927; 103415, RHB2540; 103302, SUN1925; 103281, SUN1926; 103319, SUN1927; 103303, SUN1928; 103324, SUN2536; 103283, SUN2545; 103284, SUN2546.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
Trachipteridae	*Zu cristatus*	1	1	8	L	84699, KEH8482.
Carapidae	*Echiodon drummondi*	1	1	64	A	149546, CEL7838.
Macrouridae	*Odontomacrurus murrayi*	2	2	71-240	L A	149621, CEL7826; 62187, KEH8485.
Melanonidae	*Melanonus zugmayeri*	4	5	44-69	A	149547, CEL7838; 149618, KEH8481; 147027, RHB2553; 147028, RHB2554.
Lophiidae	*Lophius piscatorius*	1	2	63	A	43152, DL63-04:015.
Oneirodidae	*Chaenophryne longiceps*	1	1	4	L	49878, RHB1045.
Ceratiidae	*Cryptopsaras couesi*	1	1	28	L	51209, RHB2547.
Scomberesocidae	*Nanichthys simulans*	1	1	38	A	150933, CEL7831.
	Scomberesox saurus	1	14	23-47	A	57652, DL63-04:013.
Exocoetidae	*Exocoetus obtusirostris*	1	1	19	L	149627, KEH8476.
Melamphaidae	*Melamphaes simus*	1	1	27	A	145320, RHB2554.
	Melamphaes typhlops	3	3	15-20	A	145512, RHB1036; 145748, RHB1915; 145513, RHB1041.
	Poromitra megalops	3	5	15-16	A	42884, CODI/ATL119; 150946, KEH8485; 146202, RHB1039
	Scopeloberyx opisthopterus	1	1	26-36	A	31621, CODI/ATL119.
	Scopelogadus beanii	2	3	19-101	A	31655, CODI/ATL119; 150944, KEH8485.
Anoplogastridae	*Anoplogaster cornuta*	2	2	123	A	31666, CODI/ATL119; 151386, RHB1039.
Diretmidae	*Diretmus argenteus*	3	4	32-37	A	83171, RHB2554; 83175, SUN1927; 83192, SUN2540.

APPENDIX 2. CONTINUED.

Family	Species	C	S	R	D	MCZ catalog number and field number
Caproidea	*Caprus aper*	2	2	35-38	A	149526, CEL7835; 149525, CEL7837.
Acropomatidae	*Howella brodiei*	5	12	18-48	A	149545, CEL7837; 49780, RHB1044; 75793, RHB1045; 86160, RHB2553, 86159, RHB2544.
Carangidae	*Naucrates ductor*	3	7	6-18	L	83806, SUN1043; 83807, SUN1044; 83808, SUN1045.
	Trachurus picturatus	5	48	11-124	A	149536, CEL7824; 149535, CEL7828; 150930, CEL7837; 149534, CEL7838; 55179, RHB1042.
Bramidae	*Brama brama*	1	1	127	A	76125, RHB2554.
Caristiidae	*Platyberyx opalescens*	1	1	20	L	150936, CEL7825.
Chiasmodontidae	*Pseudoscopelus altipinnis*	1	1	101	A	49086, RHB1039.
Centrolophidae	*Schedophilus medusophagus*	3	4	32-74	A	149614, DL63-04:014; 149613, RHB1918; 149612, RHB1920.
Nomeidae	*Cubiceps gracilis*	4	5	49-87	A	133275, RHB1918; 79269, SUN1915; 135282, SUN1918; as Aphareus obtusirostris: 32119, CODI/ATL001.
Tetragonuridae	*Tetragonurus cuvieri*	1	1	105	A	149507, CEL7834; 31667, CODI/ATL119.
Cynoglossidae	*Symphurus nigrescens*	1	1	7	L	78505, RHB1042.

B R E V I O R A

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NEW RECORDS AND DISTRIBUTIONAL AND ECOLOGICAL NOTES OF LEPTODACTYLID FROGS, *LEPTODACTYLUS* AND *ELEUTHERODACTYLUS*, FROM THE BRITISH VIRGIN ISLANDS

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ABSTRACT. Information on distribution and habitat use of frogs in the British Virgin Islands is needed for assessing population trends and status and for elucidating biogeographic patterns. We discovered 10 new populations of the four known species of Leptodactylidae on five of the 17 islands visited: *Eleutherodactylus antillensis* on Great Camanoe, Great Thatch, Jost Van Dyke, and Beef Island; *E. schwartzi* on Beef Island, Frenchmans Cay, and Jost Van Dyke; *E. cochranae* on Great Thatch and Jost Van Dyke; and *Leptodactylus albilabris* on Beef Island. We confirmed all but three previous island records: *E. cochranae* and *L. albilabris* on Virgin Gorda and an unidentified *Eleutherodactylus*, known only from the stomach of a snake, on Peter Island. The earlier *E. cochranae* record is probably in error, but *L. albilabris* and *Eleutherodactylus* seem to have disappeared from Virgin Gorda and Peter Island, respectively. The mean body size of adult males of *E. antillensis* and *E. schwartzi* was smaller on Virgin Gorda than on Tortola, and males of *E. schwartzi* were relatively large on the tiny (33 ha) island of Great Dog. On all islands except Tortola, *E. schwartzi* was almost exclusively associated with bromeliads. Island elevation and area explained 61% of the variation in the number of species when all 17 islands were included in the

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model. Elevation was the most important factor (partial $r^2 = 0.35$), whereas area explained little of the observed variation (partial $r^2 = 0.02$). The availability of specific habitat features, such as aquatic breeding sites for *L. albilabris* and retreat and nesting sites for *Eleutherodactylus,* are critical for populations on small islands. The distribution patterns in the British Virgin Islands do not indicate widespread extirpations or declines of frogs comparable to those observed in Puerto Rico and other parts of the world.

> *. . . there is an urgent need to document the distribution and abundance of amphibians.*
>
> *Leonard (1997)*

INTRODUCTION

Precipitous declines in a number of anuran populations within the past few decades have led to local extirpations and even species extinctions (Mittermeier *et al.,* 1992; Pechmann and Wilbur, 1994; Phillips, 1994; Blaustein and Wake, 1995). In Puerto Rico alone, three species of frogs (genus *Eleutherodactylus,* family Leptodactylidae) have disappeared within the past 20 years, and an additional seven show serious declines (Rivero, 1991; Joglar and Burrowes, 1996). Efforts to document and understand changes in anuran population and distribution characteristics are severely constrained by the paucity of baseline data, making it difficult to distinguish between natural population fluctuations and those caused by human activities. Furthermore, in many cases, we simply do not know where populations occurred or still occur. Knowledge of habitat requirements and factors that limit the growth of populations is also incomplete for most species of frogs in neotropical areas.

The British Virgin Islands (BVI), located on the easternmost portion of the Puerto Rico Bank in the Caribbean Sea, consist of about 50 islands, some of which are mere rocks or sand bars. During the last glacial maximum, the entire bank was united as a single land mass, which subsequently fragmented into numerous islands with the rising of sea levels (Heatwole *et al.,* 1981). Most of the islands have been isolated from each other and the rest of the bank for approximately 4,000–10,000 years (reviewed by Lazell, 1983).

Four species of leptodactylid frogs occur in the BVI: *Leptodactylus albilabris, Eleutherodactylus antillensis, E. schwartzi,* and *E. cochranae* (MacLean, 1982). All but *E. schwartz*i, which is endemic to the BVI, are widespread on the islands of the Puerto Rico Bank and also occur in Puerto Rico itself (Rivero, 1978; MacLean, 1982; Schwartz and Henderson, 1991).

Leptodactylus albilabris has a biphasic life cycle with aquatic larvae, whereas *Eleutherodactylus* species are completely terrestrial and have direct development. The distribution and habitat use patterns of all four species on the islands are poorly known, although other components of the herpetofauna of the BVI have received intensive attention over the past two decades (Mayer and Lazell, 1988; Lazell, 1983, 1991, 1995; Dmi'el *et al.,* 1996). Lazell (1983) was aware of seven populations of leptodactylid frogs on four islands of the BVI. Mayer and Lazell (1988) added two new island records, including one for an islet of only 24 ha (Frenchmans Cay). Lazell (1991) reported a previously overlooked record for the 33-ha Great Dog Island (Heatwole *et al.,* 1981), bringing the total number of known populations to 11 on seven different islands. Ten additional islands that are larger than Frenchmans Cay had not been surveyed for frogs before our study. In many cases, the survey coverage of those islands known to support frogs was incomplete.

Every October from 1993 to 1997, we investigated the distribution and ecology of leptodactylid frogs in the BVI. Based on surveys of 17 islands, we report on the distribution of *Leptodactylus* and *Eleutherodactylus* species, including new island records for 10 populations. Our objectives were to (a) compile baseline data on the distribution, habitat use, and natural history of the frogs on different islands; (b) compare present distributions to historical records; and (c) examine the pattern of distribution in relation to predictions from island biogeography (MacArthur and Wilson, 1967; Lazell, 1983).

METHODS

Survey Methods

Our operations were based on Guana Island, located ca. 0.5 km north of the east end of Tortola, BVI. The survey periods were 7–30 October 1993, 2–21 October 1994, 3–19 October 1995, 8–28 October 1996, and 8–28 October 1997. During these periods, we also visited the following islands one or more times: Tortola (14–16 October 1993; 4–6, 13–15 October 1994; 6–8, 14–15 October 1995; 11–12, 15–16, 19–20 October 1997), Beef Island (3–5 October 1995, 23 October 1996), Frenchmans Cay (7 October 1995), Virgin Gorda (26–28 October 1993, 9–11 October 1994, 17–18 October 1996), Jost Van Dyke (11–12 October 1995), Great Dog (10–11, 16 October 1996; 21 October 1997), Great Camanoe (12 October 1996), Scrub (13 October 1996), Mosquito (16–17 October 1996), Anegada (20–21 October 1996), Cooper (22–23 October 1996), Peter (24–25 October 1996, 25–26 October 1997), Great Thatch (26–27 October 1996), and Great Tobago (17–18 October 1997). We also present data for Necker and Little Thatch, where residents have been listening for frogs for several years and one of us (JL) spent several rainy nights (three nights in October 1993 on Necker and one night in October 1996 on Little Thatch).

We used visual encounter surveys, auditory transect surveys, and night driving methods to locate frogs (Heyer *et al.,* 1994). We walked along trails in likely habitats after sunset listening for calls of males, and we scanned the ground and vegetation with headlamps for frogs. In 1996, we also played recorded advertisement calls of *E. antillensis* and *E. schwartzi* to induce frogs to call. In 1995 and 1996, the use of a car allowed us to cover longer distances on larger islands (Tortola, Beef Island, Anegada, Virgin Gorda); we stopped every few minutes to listen for frog calls. For each new island record, we collected at least one voucher specimen, which was deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ).

In 1993, we systematically recorded information on each *Eleutherodactylus* heard or seen during those surveys carried out on foot and noted the following for each frog captured: species, sex, calling or not (for males), gravid or not (for females), snout–vent length (SVL), weight, microhabitat (ground, tree or bush, bromeliad, agave, herbaceous vegetation), and perch height. In 1994 and 1995, we obtained comparable information only for frogs included in a separate study on vocal behavior. In 1996, we measured the body size of *E. schwartzi* on Great Dog and Virgin Gorda to examine the hypothesis suggested by initial observations that the frogs on Great Dog were relatively large. We also measured the body size of a sample of *E. antillensis* on Guana in 1996.

To obtain additional information on habitat use and dispersion of *Eleutherodactylus,* we set up auditory transects in October 1994 on three islands (Guana, Tortola, and Virgin Gorda) and in October 1996 on Guana. In 1994, there were two transects on Guana, two on Sage Mountain, Tortola, and one on Gorda Peak, Virgin Gorda. On Guana, Transect 1 was in the north of the island along a ridge where *E. antillensis* appeared to be abundant, and Transect 2 was near the southwest tip of the island where an isolated patch of the species occurred.

The transects followed the course of relatively straight sections of existing trails or paths, which marked the middle of the transect. In 1994, each transect was 150 m long and 6 m wide. In 1996 on Guana, Transect 1 was 815 m long and Transect 2 was 300 m long. We increased their width from 6 m to 10 m, because previous observations indicated that we could accurately record all calling frogs within 5 m from the center of the transect. We placed a flag every 5 m in the center of the transect to divide it into sections of 3 × 5 m (in 1994) or 5 × 5 m (in 1996) on each side of the transect.

In 1994, we recorded the presence/absence of arboreal and terrestrial bromeliads with a crown diameter >10 cm in every 5-m × 3-m section of the transect. In 1996 on Guana, we measured habitat variables only for Transect 1. The variables measured for each 5-m × 5-m section were: (a) sum of crown diameters of bromeliads (none, not present; low, <30 cm; moderate, 30–100 cm; high, >100 cm), (b) percentage of ground covered by leaf litter, (c) depth of leaf litter/humus (measured for 152 or 47% of the 5-m × 5-m sections), and percent vegetation cover at heights of (d) <1 m, (e) 1–2 m, and (f) >2 m. The depth of the leaf litter and humus in each section was the average of three randomly located measurements obtained by poking a pencil in the leaf litter and measuring the depth of penetration. We estimated the percentage of ground covered by vegetation at different vertical layers and by leaf litter visually.

To survey frogs, two observers walked along the midline of the transect after sunset and recorded the number and species of calling males in each section of the transect. We traced the exact location of frogs only when this was required to verify their presence within the transect boundaries. In 1994, we surveyed the transects for frogs on Guana on four consecutive nights (17–18, 18–19, 19–20, and 20–21 October). Transect 1 was surveyed twice each night on two nights and three times on one night to obtain information on the consistency of the number of calling frogs within nights. Transect 2 was surveyed once on 18 October. In 1996, we surveyed Transect 1 once each on 18 and 25 October and twice on 28 October. Transect 2 was surveyed once (on 18 October). We surveyed both transects on Tortola twice on 13 October 1994 and the transect on Virgin Gorda once on 10 October 1994. We checked transects only on nights when rain had fallen during the 24-hour period prior to the search, and conditions were favorable for calling.

Data Analysis

We used a multiple regression analysis to examine the effects of island size and elevation on the number of species present. We also applied multiple regression to a reduced data set that excluded both islands that contained the full complement of four species (Tortola and Jost Van Dyke) to include the distance from potential source populations in the analysis. The source for island size and elevation was Lazell (1983). The distance to the nearest potential source population was measured as the shortest distance between an island and either Tortola, Jost Van Dyke, or Virgin Gorda, whichever distance was shortest.

We used one-way ANOVA to examine differences in body size of adult male *E. antillensis* and *E. schwartzi* among years. We also used ANOVA to compare SVL of *E. antillensis* and *E. schwartzi* among years and islands.

We calculated the variance/mean ratio as an index of dispersion of calling males of *E. antillensis* in 5-m and 50-m sections of Transect 1 on Guana in 1996 and used the χ^2 test to determine whether the pattern was significantly different from random (Krebs, 1989). We performed a multiple regression analysis to examine the effects of habitat variables, measured in each 5-m × 5-m section of the transect, on the number of calling frogs on Guana on 28 October 1996, when the number of frogs was the greatest. We also performed the same analysis using the number of 5-m × 5-m sections with frogs (1) and without frogs (0) as the dependent variable. The value for each section of the transect in the second case was determined based on whether calling frogs were found within a transect section during any of the four surveys in 1996.

DISTRIBUTION

Species Diversity

The number of species per island varied from zero to four (Table 1). Only two islands, Tortola and Jost Van Dyke, contained the full complement of four species. One island had three species, three had two, and four had one. We found no frogs on the remaining seven islands.

Area and elevation explained 60.7% of the variance in the number of species among islands (multiple regression: $F_{2,14} = 10.8$, $P = 0.002$). Elevation explained most of this variance (simple $r = 0.76$, partial $r^2 = 0.35$), whereas island area contributed very little to the model (simple $r = 0.51$, partial $r^2 = 0.02$). When the two islands with the full complement of species were deleted from the analysis and the distance to nearest potential source population was added as an independent variable, the model was marginally significant ($r^2 = 0.51$, $F_{3,11} = 3.79$, $P = 0.04$). In this model, island area (simple $r = 0.22$, partial $r^2 = 0.25$) and distance to a potential source population (simple $r = -0.007$, partial $r^2 = 0.21$) explained most of the variance, whereas the contribution of elevation was small (simple $r = 0.50$, partial $r^2 = 0.001$).

Leptodactylus albilabris

We found *L. albilabris* on four of the 17 islands: Beef, Tortola, Jost Van Dyke, and Anegada (Table 2). This species had not been previously documented from Beef (372 ha), separated from Tor-

TABLE 1. NUMBER OF SPECIES OF FROGS IN RELATION TO ISLAND AREA, ELEVATION, AND DISTANCE FROM A POTENTIAL SOURCE POPULATION. ISLAND AREA AND ELEVATION ARE FROM LAZELL (1983). DISTANCES FOR EACH ISLAND WERE MEASURED EITHER FROM TORTOLA, JOST VAN DYKE, OR VIRGIN GORDA (WHICHEVER DISTANCE WAS SHORTEST).

Island	No. of Species	Area (km²)	Elevation (m)	Distance to Potential Source Population (km)
Tortola	4	5,444	521	NA
Anegada	1	3,872	8.5	32.5 (Tortola)
Virgin Gorda	2	2,130	414	11.7 (Tortola)
Jost Van Dyke	4	840	398	NA
Peter	0	429	177	5.5 (Tortola)
Beef	3	372	244	0.1 (Tortola)
Great Camanoe	1	337	187	2.1 (Tortola)
Guana	1	297	266	0.5 (Tortola)
Cooper	0	138	155	6.8 (Tortola)
Great Thatch	2	123	187	0.7 (Tortola)
Scrub	0	97	141	3.7 (Tortola)
Great Tobago	0	87	147	4.0 (Jost Van Dyke)
Mosquito	0	50	95	17.7 (Virgin Gorda)
Great Dog	1	33	89	11.1 (Virgin Gorda)
Necker	0	30	32	22.0 (Virgin Gorda)
Frenchmans Cay	2	24	131	0.1 (Tortola)
Little Thatch	0	24	100	0.5 (Tortola)

tola by a ca. 100-m wide channel. Our attention was first called to the presence of *L. albilabris* on this island by Dr. Gregory Mayer, who reported hearing calls and locating tadpoles, which were inspected by one of us (JL), in temporary pools among rocks in scrub vegetation several years ago. We did not locate this site but found *L. albilabris* in muddy ditches around the airport (MCZ 124777–81, 125954). In 1995, we located several males calling from inside tufts of grass and from small cavities in the mud banks close to the water's edge, as well as many metamorphosed juveniles. We did not hear calls of *L. albilabris* east of the airport.

On Tortola, we heard calls of *L. albilabris* from roadside ditches throughout the island and from small pools on Sage Mountain (MCZ 107339, 110992–5, 117677). On Jost Van Dyke, we heard

L. albilabris in a riverbed by Old Hill west of White Bay and in a marshy site in the town of Great Harbour (MCZ 110990–1).

On Anegada, we found several concentrations of *L. albilabris* in an area called the Slob, ca. 1.5 km northwest of the airport (MCZ 125953). The frogs were in wet areas under dense shrubs on coral-limestone substrate covered by leaf litter and humus. Several males were calling from land crab holes, and we also saw many metamorphosed juveniles.

We did not find *L. albilabris* on any of the other islands, including Virgin Gorda, which we visited in three different years. In 1993 and 1994, our surveys were confined to Gorda Peak, but in 1996, we spent many hours driving around the island after sunset during and after rain. Extensive pools were present on Gorda Peak in 1993, but these were dry in 1994 and contained little water in 1996. Roadside ditches, where these frogs commonly occurred on Tortola, contained water, but we detected no frogs. Small, temporary freshwater puddles were present on Great Camanoe.

Eleutherodactylus antillensis

We found *E. antillensis* on eight of the 17 islands visited: Virgin Gorda, Great Camanoe, Guana, Beef, Tortola, Frenchmans Cay, Great Thatch, and Jost van Dyke (Table 2). The species has not been previously reported from Great Camanoe, Great Thatch, or Beef (MCZ 132823). In addition, we have found no previous records of *E. antillensis* from Jost Van Dyke, although MacLean (1982) reported the distribution of the species to encompass "all major islands" of the Virgin Islands. On Jost Van Dyke, calling males of *E. antillensis* were patchily distributed in areas west of White Bay toward Old Hill and east to Great Harbour, including the town site (MCZ 124786). On Great Camanoe, we located frogs in the hills on the southwest portion of the island (MCZ 125949). On Great Thatch, we found *E. antillensis* throughout the densely vegetated south slope of the island (MCZ 125950).

Eleutherodactylus schwartzi

We located *E. schwartzi* on six of the 17 islands visited: Virgin Gorda, Great Dog, Beef, Frenchmans Cay, Tortola, and Jost Van

TABLE 2. RECONFIRMED, UNCONFIRMED, AND NEW ISLAND RECORDS FOR LEPTODACTYLID FROGS IN THE BRITISH VIRGIN ISLANDS.[a]

		Species			
Island	Survey Dates	New Record	Previous Record Confirmed	Previous Record Not Confirmed	Source of Previous Records
Anegada	20–21 Oct. 1996	—	La	—	MacLean, 1982
Virgin Gorda	26–28 Oct. 1993 9–11 Oct. 1994 17–18 Oct. 1996	—	Ea, Es	Ec, La	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)
Great Dog	10–11, 15 Oct. 1996 21 Oct. 1997	—	Es	—	Heatwole *et al.*, 1981
Great Camanoe	12 Oct. 1996	Ea	—	—	—
Guana	7–30 Oct. 1993 2–21 Oct. 1994 9–19 Oct. 1995 8–18 Oct. 1996 8–28 Oct. 1997	—	Ea	—	Mayer and Lazell, 1988; Lazell, 1991
Beef Island	3–5 Oct. 1995 23 Oct. 1996	Es, La, Ea	—	—	
Tortola	14–16 Oct. 1993 4–6, 13–15 Oct. 1994 6–8, 14–15 Oct. 1995 11–12, 15–16, 19–20 Oct. 1997	—	Ea, Es, Ec, La	—	MacLean, 1982 (all 4 spp.); Schwartz and Henderson, 1985 (Es)

TABLE 2. CONTINUED.

Island	Survey Dates	Species			Source of Previous Records
		New Record	Previous Record Confirmed	Previous Record Not Confirmed	
Peter Island	24–25 Oct. 1996 25–26 Oct. 1996	—	—	E. sp.	Henderson and Sadjak, 1996 (*Eleutherodactylus* in stomach of snake)
Frenchmans Cay	7 Oct. 1995	Es	Ea	—	Mayer and Lazell, 1988 (Ea)
Great Thatch	26 Oct. 1996	Ea, Ec	—	—	—
Jost Van Dyke	11-12 Oct. 1995	Ea, Es, Ec	La	—	Schwartz and Thomas, 1975 (La); MacLean, 1982 (La)

[a] Ea, *Eleutherodactylus antillensis*; Ec, *E. cochranae*; Es, *E. schwartzi*; La, *Leptodactylus albilabris*; E. sp, unidentified species of *Eleutherodactylus*.

Dyke (Table 2). The presence of this species on Beef, Frenchmans Cay, and Jost Van Dyke was previously undocumented. On Beef, we found *E. schwartzi* along the road that transects the island and in a patch of terrestrial bromeliads (*Bromelia pinguin*) along a path that diverges from the main road near its northern end (MCZ 124782).

On Frenchmans Cay, we heard calls of *E. schwartzi* from gardens along the road east from the bridge to Tortola (MCZ 124783). On Jost Van Dyke, we heard calls of scattered *E. schwartzi* from gardens, pastures, and gullies in and around Great Harbour (MCZ 124785).

In 1996, we confirmed the presence of *E. schwartzi* on Great Dog Island (MCZ 125946–8), an islet of 33 ha, first reported by Heatwole *et al.* (1981). Numerous frogs were present in a ca. 13-m × 16-m patch of bromeliads, *Hohenbergia antillana,* located near the peak of the ridge that extends along the length of the island. In addition, on the night of 10–11 October 1996, we heard a single male calling near the beach in dense vegetation on the south side of the island ca. 500 m from this patch. We located five egg clutches of *E. schwartzi* on 10 October within bromeliads (Ovaska *et al.,* 1998).

We observed numerous *E. schwartzi* on Sage Mountain, Tortola, and on Gorda Peak, Virgin Gorda, and we also heard calls and observed frogs in other areas of these two islands (MCZ 107340–1, 115830–8, 117567–9, 117688–92, 119247–51, 116273, 124784, and U.S. National Museum of Natural History 329482–91).

Eleutherodactylus cochranae

We located *E. cochranae* on three of the 17 islands visited: Tortola, Jost Van Dyke, and Great Thatch (Table 2). The species has not previously been reported from Jost Van Dyke or Great Thatch. Based on advertisement calls by males, *E. cochranae* was the most widely distributed and abundant frog species in the areas surveyed on Jost Van Dyke (MCZ 124787–8). These included areas west from White Bay toward Old Hill and east to Great Harbour. Calling males were perched on cacti, trees, and arboreal and terrestrial bromeliads.

On Great Thatch, we surveyed the southern slope of the densly vegetated island and captured *E. cochranae* (MCZ 125951). On Tortola, we captured *E. cochranae* on Sage Mountain (MCZ 116269–71) and also heard advertisement calls from other forested locations, including sites near sea level. We did not hear calls of *E. cochranae* on Frenchmans Cay, a 24-ha islet separated from Tortola by a channel <10 m wide, although males were calling in adjacent areas on Tortola on the same night.

We also did not find *E. cochranae* on Virgin Gorda, although we searched for it several times in 3 years (1993, 1994, and 1996). MacLean (1982) lists this species from Virgin Gorda, but we have been unable to locate a voucher specimen or any other report of its occurrence there.

BODY SIZE OF *ELEUTHERODACTYLUS*

The SVL of calling males of *E. antillensis* did not show significant differences among years on any of the islands examined, although males tended to be smaller on Tortola in 1994 than in 1993 and 1995 (Guana: $F_{3,48} = 1.67$, $P = 0.19$; Tortola: $F_{2,49} = 3.07$, $P = 0.06$; Virgin Gorda: $F_{1,57} = 0.18$, $P = 0.67$). Similarly, there were no significant differences in SVL of *E. schwartzi* among years (Tortola: $F_{1,16} = 0.01$, $P = 0.90$; Virgin Gorda: $F_{2,36} = 0.38$, $P = 0.68$). The data for all years were therefore combined for analyses of interisland differences.

The average SVL of adult male *E. antillensis* varied among Guana, Tortola, and Virgin Gorda ($F_{2,141} = 24.9$, $P < 0.001$; Fig. 2). Males on Virgin Gorda were smaller ($\bar{x} = 27.2$ mm) than those on Guana ($\bar{x} = 29.3$ mm) and Tortola ($\bar{x} = 29.2$ mm). The average SVL of calling males of *E. schwartzi* also differed among islands ($F_{2,71} = 29.4$, $P < 0.001$; Fig. 1). Males were the smallest on Virgin Gorda ($\bar{x} = 22.3$ mm), largest on Great Dog Island ($\bar{x} = 25.6$ mm), and intermediate on Tortola ($\bar{x} = 23.8$ mm).

The average weight of calling males of *E. antillensis* was 1.7 g (SD = 0.1, $n = 51$; 1993–96 combined) on Guana, 1.3 g on Virgin Gorda (SD = 0.2 g, $n = 58$; 1993–94 combined), and 1.7 g on Tortola (SD = 0.3, $n = 52$; 1993–95 combined). The average weight of calling males of *E. schwartzi* was 0.9 g (SD = 0.2 g, $n = 16$; 1993 and 1994 combined) on Tortola, 0.8 g (SD = 0.1

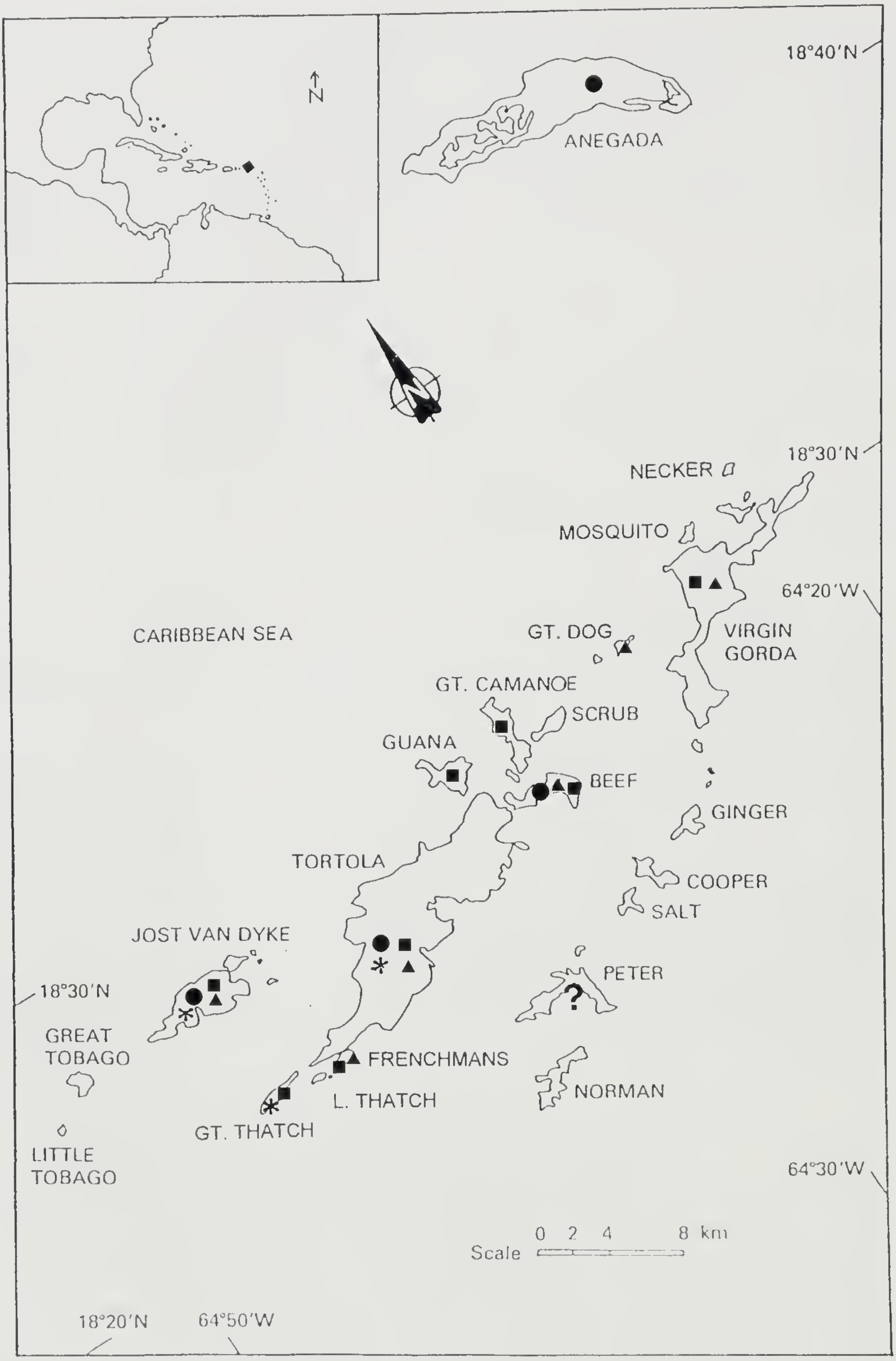
N
18°40'N
ANEGADA
NECKER
18°30'N
MOSQUITO
64°20'W
VIRGIN GORDA
GT. DOG
CARIBBEAN SEA
GT. CAMANOE
SCRUB
GUANA
BEEF
GINGER
TORTOLA
COOPER
SALT
JOST VAN DYKE
PETER
?
18°30'N
GREAT TOBAGO
FRENCHMANS
L. THATCH
NORMAN
GT. THATCH
LITTLE TOBAGO
64°30'W
0 2 4 8 km
Scale
18°20'N
64°50'W

Figure 1. Map of the British Virgin Islands indicating major islands and those mentioned in the text. Insert shows the position of the these islands in the Caribbean. ● *L. albilabris,* ■ *E. antillensis,* ▲ *E. schwartzi,* ✻ *E. cochranae.*

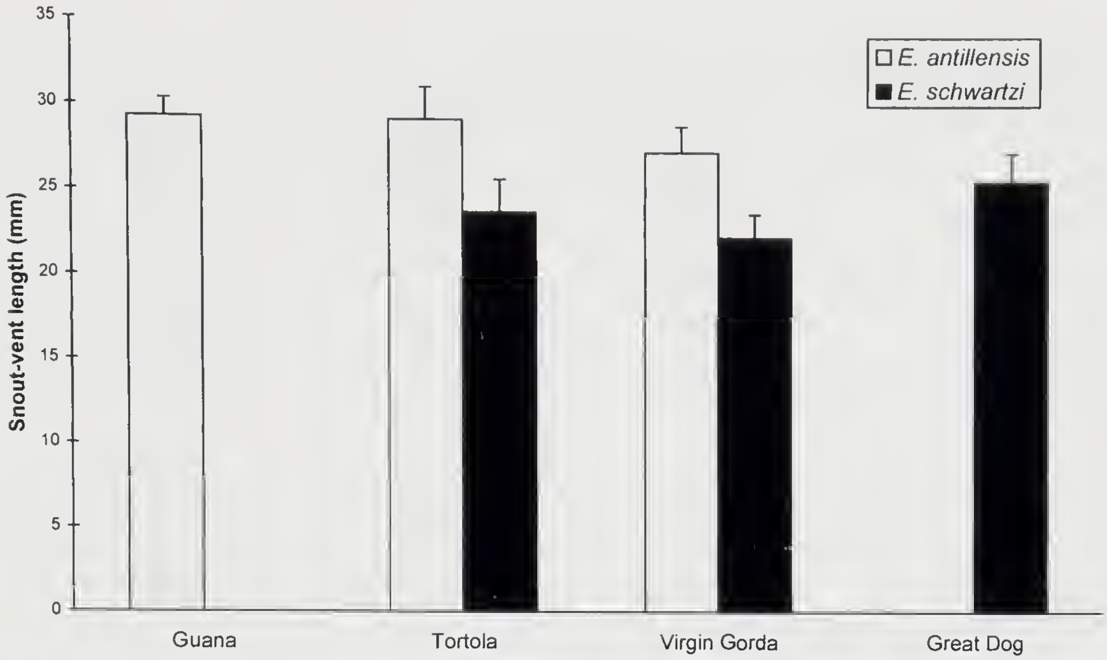

Figure 2. Snout–vent length (SVL) of calling males of *Eleutherodactylus antillensis* and *E. schwartzi* from Guana, Tortola, Virgin Gorda, and Great Dog. Mean, top of bars; 1 SD, vertical lines.

g, *n* = 39; 1993, 1994, and 1996 combined) on Virgin Gorda, and 1.2 g (SD = 0.2 g, *n* = 17; 1996) on Great Dog.

Both species were sexually dimorphic with respect to body size, females being larger than males. The SVL of 14 female *E. antillensis* measured in 1993 was 33.8 mm (SD = 4.6 mm, range = 28.0–43.2) and their weight was 2.7 g (SD = 1.2 mm, range = 1.2–4.8 g; all islands combined). Ten female *E. schwartzi* were 31.2 mm in SVL (SD = 3.0 mm, range = 25.5–35.5 mm) and weighed 1.9 g (SD = 0.4 g, range = 1.2–2.7 g).

HABITAT USE BY *ELEUTHERODACTYLUS*

Eighty-nine percent of all male *E. schwartzi* (*n* = 45) and 74% of male *E. antillensis* (*n* = 171) located in October 1993 were perched in vegetation <2.5 m high while calling (data for Tortola, Virgin Gorda, and Guana combined). The remaining 11% of calling *E. schwartzi* and 26% of *E. antillensis* were perched higher than 2.5 m and thus were out of our reach. We did not capture *E. cochranae* in 1993, although we audiotaped calls of this species on Tortola. In 1994, we captured nine *E. cochranae* (eight males and one female) at heights below 2.5 m on Sage Mountain, Tortola, but traced most calling males to perch sites well above our reach in trees. In contrast, we frequently observed *E. cochranae* (calling males, noncalling adults, and juveniles) in vegetation <2.5 m high in October 1995 after high winds associated with Hurricanes Louis and Marilyn in September had visibly altered the habitat, knocking down many trees and stripping leaves off of those left standing; however, we did not systematically record perch heights.

While calling, males of *E. antillensis* were most frequently perched on leaves or branches of trees and shrubs on Guana (60% of 94 observations), Tortola (68% of 53 observations), and Virgin Gorda (84% of 79 observations; data for 1993–95 combined for all islands). Males also called from herbaceous vegetation (Tortola: 28%; Virgin Gorda: 4%), terrestrial and arboreal bromeliads (Guana: 14%; Virgin Gorda: 4%), and agave plants (Guana: 24%). On Tortola, calling *E. schwartzi* were perched on trees or shrubs (75% of 16 recordings) and herbaceous vegetation (25%). In contrast, the majority of observations of calling *E. schwartzi* on Virgin Gorda were from bromeliads (84% of 45 recordings), followed by trees and shrubs (13%) and herbaceous vegetation (2%).

When examined in relation to the availability of bromeliads along auditory transects in 1994, the distribution of calling males of *E. antillensis* and *E. schwartzi* differed significantly from random on Virgin Gorda but not on Tortola (Table 3). On Virgin Gorda, males of *E. schwartzi* were restricted to sections of the transect that contained bromeliads. In contrast, male *E. antillensis* were not associated with bromeliads either on Virgin Gorda or Tortola (Table 3). On Guana, male *E. antillensis* were found exclusively in sections of Transect 2 containing bromeliads, but the relationship was not statistically significant based on habitat availability, due to the small sample size (Table 3). The frogs were most abundant on Transect 1, where bromeliads were present in every section, thus precluding a similar analysis.

On Guana in 1996, calling males of *E. antillensis* were aggregated among 5-m × 10-m sections of the transect during all but one check (Table 4). On a larger scale, when the transect was

Table 3. Number of calling males of *Eleutherodactylus antillensis* and *E. schwartzi* on Virgin Gorda, Tortola, and Guana in October 1994.[a]

Island (Transect No.)	Bromeliads Present	Bromeliads Absent	Total	X^2	*P*
Virgin Gorda (1)				23.1	<0.01
No. of *E. antillensis*	12	22	34		
No. of *E. schwartzi*	18	0	18		
No. of Sections	24	36	60		
Tortola (1 + 2)				5.2	<0.1, >0.05
No. of *E. antillensis*	11	18	29		
No. of *E. schwartzi*	19	11	30		
No. of Sections	50	70	120		
Guana (2)				3.5	<0.1, >0.05
No. of *E. antillensis*	10	0	10		
No. of Sections	44	16	60		

[a] Counted in 3- × 5-m sections of auditory transects in relation to the presence of bromeliads.

Table 4. Dispersion of calling male *E. antillensis* along a 10 × 815-m transect (Transect 1 in text) on Guana Island in October 1996.

	Transect Divided into 5 × 10-m Sections (no. sections = 163)			Transect Divided into 10× 50-m Sections (no. sections = 16)[1]		
Date	Variance/Mean Ratio	X^2	*P*	Variance/Mean Ratio	X^2	*P*
18 Oct.	1.2	196.4	<0.05	2.6	39.5	<0.001
25 Oct.	1.3	208.4	<0.05	2.8	42.3	<0.001
28 Oct. (Check 1)	1.7	281.2	<0.05	6.2	92.9	<0.001
28 Oct. (Check 2)	1.2	192.1	>0.05	3.1	47.0	<0.001

[1] The last 15 m was omitted from the analysis to achieve equal division of the transect.

divided into 50-m × 10-m sections, calling males were highly aggregated during each check. The habitat attributes measured explained little of this dispersion. The number of calling males was significantly correlated with the habitat variables both when only data for the night with the most calling frogs (74 frogs on first transect check on October 28; $F_{6,143} = 2.95$, $P < 0.01$) were included and when each section of the transect was scored based on whether or not it was used by frogs during any of the checks ($F_{6,143} = 5.67$, $P < 0.001$). In both cases, the correlations were weak ($r^2 = 0.11$ and 0.19 for the two models, respectively).The partial r^2 for the habitat variables in the better, second model ranged from 0.007 to 0.054 and were the highest for the sum of crown diameters of bromeliads (0.045) and percent substrate covered by leaf litter (0.054).

DISCUSSION

We found 10 previously unreported populations of leptodactylid frogs on five islands (Great Camanoe, Beef, Frenchmans Cay, Great Thatch, and Jost Van Dyke) and confirmed all but three of previous records from the BVI. Demonstrating the absence of a species is always problematic, and these small frogs are inconspicuous when not calling and could be missed easily. The month of October, however, is generally favorable for locating frogs, because, together with November, it has the highest average rainfall per month (6.44 and 6.57 inches of rain in October and November, respectively, based on weather records from 1960 to 1984 obtained from Water and Sewage Department and Planning Division, Road Town, Tortola, and compiled by A. Swain). Rainfall is probably the most important factor affecting activity by *Eleutherodactylus* species in the BVI, although activity is also likely to take place on humid, rainless nights. It was not always possible, however, to time our visits to the different islands during or immediately after rain. Our confidence that we located all species is greatest for small islands that we visited repeatedly, such as Guana. We are also highly confident that there are no native frogs on either Necker or Little Thatch, because no frogs have ever been seen or heard there either by us or by residents. The only amphibian ever found on Necker was the introduced *Hyla (Osteopilus) septentrionalis,* which was collected there on 19 October 1993 from a crack in a recently imported wooden beam (MCZ 119258).

Two of the three previous records that we failed to confirm were from Virgin Gorda (*E. cochranae* and *L. albilabris*; MacLean, 1982), and the remaining record was from Peter Island: an unidentified *Eleutherodactylus* found in the stomach of a snake, *Liophis* (*Alsophis*) *portoricensis* (Henderson and Sadjak, 1996). This snake (MCZ 37303) was collected by Chapman Grant on 14 August 1932. The frog, uncataloged, was sent to the late Albert Schwartz for identification, but R. W. Henderson (personal communication) subsequently was unable to locate it in Schwartz's materials.

On Peter Island in 1996, we walked throughout the inhabited, eastern part of the island at night, and in 1997 we spent a rainy night on the south side of the western part of the island investigating a verdant gully, which to us appeared the best site for locating frogs. *Eleutherodactylus* seems to have disappeared from Peter Island at some time since 1932. On Virgin Gorda, we covered much of the island at night in the rain in three different years, including likely habitats on Gorda Peak (but excluding the roadless, easternmost portion of the island). We have found no records other than MacLean (1982) of either *E. cochranae* or *L. albilabris,* nor have we been able to locate voucher specimens. Furthermore, MacLean *et al.* (1977) do not report *E. cochranae* or *L. albilabris* from Virgin Gorda, raising suspicions about the 1982 listings. We conclude that the record for *E. cochranae* on Virgin Gorda is in error and that there is no evidence that the range of this species extends east of Tortola. We cannot, however, conclusively dismiss the possible former presence of *L. albilabris* on the island based on accounts of residents, who remember "ditch frogs" in and around Spanish Town many years ago before the extensive ponds were drained for the construction of a marina and a hotel.

When all 17 islands visited were considered, elevation and area explained much of the variation (61%) in the number of species among islands, with elevation being the most significant factor. The importance of elevation in biogeographical patterns of small islands was emphasized by Lazell (1983), and our data support this hypothesis. Our data also show that even very small islands, such as Frenchmans Cay, a mere 24 ha, can support at least two species of frogs. Frenchmans Cay is relatively high, 131 m, which might allow it to support more species than expected based on area alone. Both Frenchmans Cay and Beef, however, are separated from Tortola by narrow, bridged channels. Frogs dispersing in the rain can easily cross such bridges (JL, unpublished data from New England and China). Therefore, the number of species on these islands may reflect repeated colonizations from Tortola rather than permanent populations. The reconfirmation of *E. schwartzi* from Great Dog Island, an islet of only 33 ha located at least 3 km from the nearest potential colonization source (Virgin Gorda), shows that this species can persist on very small islands, provided suitable moist microhabitats, such as bromeliads, are present.

Leptodactylus albilabris, which has an aquatic larval stage, can be expected to be absent from islands that do not have suitable water bodies for breeding. Apart from temporary pools on Gorda Peak, drainage ditches (mostly paved) in Spanish Town on Virgin Gorda, and small freshwater puddles on Great Camanoe, we did not observe potential aquatic breeding habitats on the islands where we failed to locate this species.

Stewart and Pough (1983) showed experimentally that the availability of retreat and nest sites can limit population growth of *E. coqui* in Puerto Rico. Terrestrial and arboreal bromeliads, plants that hold moisture in their leaf axils, may provide such sites for terrestrially breeding forest frogs. Of the three species of *Eleutherodactylus* that we studied, *E. schwartzi* was most closely associated with bromeliads, an association also pointed out by Schwartz and Henderson (1991). On all islands except Tortola, we found *E. schwartzi* almost exclusively in terrestrial and arboreal bromeliads. Broader habitat use on Sage Mountain, Tortola, can be explained by the relatively high rainfall and dew that this highest point in the Virgin Islands receives. On Great Dog, we found *E. schwartzi* nests with egg clutches only in a small patch of terrestrial bromeliads, which most likely facilitated the persistence of the population.

Eleutherodactylus antillensis and *E. cochranae* used a variety of microhabitats in addition to bromeliads. Most male *E. antillensis* called from perch heights <2.5 m in vegetation. Previously, Rivero (1978) and Henderson and Schwartz (1991) also noted that males often called from low vegetation. We observed *E. cochranae* using cavities in tree trunks and branches for calling, retreat, and nest sites (Ovaska and Caldbeck, 1997, and unpublished data). Most calling male *E. cochranae* were high in the trees, thus limiting our access to this species. Schwartz and Henderson (1991) stated that males call from 1 m (3 ft) above ground to high in the trees. According to Schwartz and Henderson, the species occurs primarily in xeric forests. On Tortola, however, we found *E. cochranae* together with *E. schwartzi* and *E. antillensis* in mesic forest on Sage Mountain. The habitat on Great Thatch was also mesic, and only Jost Van Dyke could be characterized as mainly xeric.

Eleutherodactylus antillensis was the most widespread of the three species. Although not associated with bromeliads on the relatively wet islands of Tortola and Virgin Gorda, the presence of bromeliads appeared to become more important with increasing aridity. On the relatively dry island of Guana, the frogs were associated with sites that contained bromeliads and abundant leaf litter, although these factors explained only a little of the spatial dispersion of frogs along transects. Abundant leaf litter might be important for breeding, as all nests of this species that we have found have been under leaf litter (Ovaska and Caldbeck, 1997, and unpublished data).

The mean body size of adult males of both *E. antillensis* and *E. schwartzi* differed among islands. Woolbright (1989) found that the growth of male *E. coqui* in the field ceased after reproductive maturity was attained. Furthermore, the period of growth could be extended in the laboratory under conditions that were unfavorable for breeding, thus resulting in greater maximum body size. Therefore, frogs that live under social or environmental conditions that favor the early attainment of reproductive maturity can be expected to be relatively small. The selective pressures responsible for the observed patterns in body size among islands cannot be resolved from our data, and studies that specifically address this question are desirable. The differences were consistent among years, indicating that the operational factors are persistent over time.

There are six islands larger than Frenchmans Cay in the BVI that have not been surveyed for frogs (Prickly Pear, Ginger, Salt, Norman, and Little Jost Van Dyke). All, however, are relatively dry and might not be suitable for frogs. Additional populations that were undetected by us may also continue to be discovered on the islands that we surveyed. Nevertheless, our study provides baseline data that may become increasingly important because of regional and global changes in climate patterns.

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